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LATITUDINAL DIFFERENCES IN GROWTH RATES OF SOME INTERTIDAL MARI--ETC(U)

JUN 69 J B LEWIS, F AXELSEN, I GOODBODY

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LATITUDINAL DIFFERENCES
IN GROWTH RATES OF
SOME INTERTIDAL MARINE MOLLUSCS
IN THE CARIBBEAN.

⑨ Status rept.

by
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Cynthia Page⁴, Geoffrey Chislett⁵
and Michael Choudhury⁶

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LATITUDINAL DIFFERENCES IN GROWTH RATES
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INTRODUCTION

The growth rates of a great many littoral marine animals living in temperate and cold climates have been investigated. Literature concerning intertidal forms has been reviewed by Moore (1958) and Newell (1964), while Wilbur and Owen (1964) have assembled information on mollusc growth. Growth rates of marine tropical and subtropical forms are, however, comparatively little known.

Growth rates and other aspects of the ecology of a number of tropical animals in Barbados, West Indies, have been investigated (Lewis, 1958, 1960, 1961, 1963, 1966). Similarly at Miami growth rates of a series of tropical forms have already been studied (Moore et al., 1963a, 1963b; Macpherson 1965, 1968; Lenderking 1954; Kolipinski 1964). Goodbody (1962, 1963) has investigated ascidian growth rates in Jamaica while growth of littoral forms in Puerto Rico has been studied by J. Randall (1964) and H. Randall (1964).

These studies indicate that different rates of growth may be found for the same species within the Caribbean. For example, the sea urchin Tripneustes matures in a single year in Barbados and reaches a size of 8 cm test diameter (Lewis 1958), while at Miami it appears to grow a little more slowly and to mature first at a slightly greater size. Both this species and the urchin Lytechinus variegatus grow faster at Miami in the winter than in summer (Moore et al., 1963a, 1963b). There appear, then, to be latitudinal variations in growth rates in the Caribbean. It is the purpose of the present study to consider to what extent latitudinal differences in growth rates may exist in some intertidal molluscs in the Caribbean.

A recent paper by Ansell (1968) on the growth of the hard clam Mercentaria showed that in the north of its range, growth takes place only during the summer, while further south growth is continuous during the year. Growth stopped when environmental temperatures were below 9°C and above 30°C . An optimum temperature of 20°C was indicated for growth and the relationship between temperature and growth appeared the same throughout the geographical range. Considerable local variations in growth rates were recorded and factors other than temperature were suggested as limiting growth. Similarly, Dehnell (1955) found considerable compensation for low temperatures at the northern end of a geographical species range and suggested that a number of factors influenced geographical differences in growth rates.

Many factors are known to affect growth rates of molluscs. Gonad maturation, age, temperature, food supply, environmental and biotic factors all have been shown to alter growth rates (Russell 1909; Orton 1911, 1928; Allee 1930; Moore 1938; Thompson 1942; Fox and Coe 1942, 1943; Carter 1951; Quayle 1951; Dehnell 1955; Orton et al. 1956; Williams 1964a, 1964b; Frank 1965a, 1965b, 1965c, 1969).

The reduction in growth rate during gonad maturation is presumed to be due to the energy loss required to elaborate gonads and sex products. Lawrence, Lawrence and Giese (1965) worked with chitons and found there was an inverse relation between digestive gland growth and gonad cycles. They suggested that nutritive demands of gonad growth might be a factor in the reduction in size of the digestive gland. It was not possible to say whether gonad growth

was due to direct transfer of stored material from the digestive gland. These workers did, however, comment on the very close association between the gonad and the digestive gland in molluscs and noted that the digestive gland is an organ of energy storage.

Orton (1920) and Moore (1958) have suggested that continuous breeding is common in the tropics. It is inferred that fluctuations of growth rates, caused by the seasonal gonad maturation, is therefore not significant. In some animals, even though there are definite pronounced breeding seasons, there appears to be no reduction in growth rate (Loosanoff and Nomejko 1949; Quayle 1951; Leighton and Boolootian 1963; Williams 1964b).

The effects of temperature on growth rates of molluscs have been considered by several workers (Russell 1909; Quayle 1951; Taylor 1959, 1960; Williams 1964a, 1964b; Kolipinski 1964). In most cases the growth rates increased with increasing temperatures. It has also been found, however, that excessively high temperatures can, if prolonged, cause death. Mayer (1914) stated that the effect of increased temperature is felt to a greater extent in tropical animals than in temperate or arctic forms. This, he concluded, was probably due to the fact that tropical animals live within 10° to 15°C of their upper death temperature.

Thorson (1936) and Dehnel (1955) have found, however, that larval growth of arctic molluscs is faster than forms from more southerly latitudes. This appears to be an adaptation of these northern pelagic animals to allow them to take full advantage of the short production season in the arctic.

It has been generally recognized that growth rates decrease with increasing age (Carter 1951). In some cases, growth has been shown to cease after sexual maturity has been reached. Moore (1938) found this to be the case in the gastropod Purpura lapillus.

Food supply and its effect on growth rate has been investigated by Fox and Coe (1942, 1944), Leighton and Boolootian (1963) and Frank (1965a, 1965b). It was found that abundant food supplies, efficiency in foraging, an increase in time available for feeding and food of high nutritive value all produced increases in growth rate.

Several authors (Colman 1933; North 1954; Moore 1958; Meyer and O'Gower 1963; Lewis 1964, and others) have recognized the great influence of wave action on distribution and zonation of organisms in the intertidal habitat. Changes in shell shape and size accompanying increasing exposure have been noted by several researchers (Russell 1909; Orton 1914; Abe 1932; Moore 1934; Segal 1956; Wara and Wright 1964; Williams 1964a; Frank 1965a). The majority of authors have inferred that the higher living intertidal animals developed thicker shells and exhibited slower growth rates than forms occurring lower on the shore.

Biotic factors, such as competition and crowding, have been suggested (Allee 1930; Connell 1961; Frank 1965a; Forster 1967) as causing decreased growth rates.

Several reports on the growth rates of members of the gastropod family Neritidae have been documented. Woodward (1892) described the mode of growth and the structure of the shell of Velates conoideus (Lam.) and other Neritidae. Andrews (1935) studied shell repair in Neritina.

Kolipinski (1964) described the life history, growth, and ecology of four Nerita species. Recently Axelsen (1968) and Chislett (1969) studied the growth rates of three species of Nerita in Barbados.

MATERIALS AND METHODS

Six species of intertidal gastropods which are common throughout the Caribbean were chosen for study. They were Littorina ziczac Gmelin, Nodolittorina tuberculata Menke, Tectarius muricatus Linne, Nerita peloronta Linne, Nerita versicolor Gmelin and Nerita tessellata Gmelin.

The growth rates of the six species considered were determined by two methods; by the recapture and measurement of marked individuals and by the determination of size frequency distributions from random samples. At approximately monthly intervals, between 300 and 500 specimens of each species were collected from the various stations in Barbados and Jamaica. These samples were collected at random from along a line perpendicular to the shore from the lower to upper limit of each species. All the individuals in this transect were collected and although the sample was not taken from the same position each month, it was collected in the same area. The maximum shell length (Kolipinski 1964) of each animal was measured to the nearest 0.1 mm with a micrometer. All animals were returned to the sampling area when the measurements were completed.

Marking of individual animals was accomplished by attaching small numbered plastic tags to the shells by means of an epoxy resin glue. The tags were supplied by the Howitt Plastics Co. of Molalla,

Oregon. They were of dimensions $1/16'' \times 1/8''$ with serial numbers from 1 to 999 stamped in black on them. Several colours were available. The cement took several hours to dry, after which the animal was returned to the point of collection. Marked specimens were recovered each month, remeasured and returned to the point of capture. Approximately 1000 of each species were marked at each field station.

Standard statistical procedures (Stanley 1963) were used throughout for the analysis of population structure and growth rates. The details of these procedures are noted in the relevant sections of the report.

FIELD STATIONS - BARBADOS

Four main stations were chosen for this study, at Little Bay, Heywood's Beach (Six Men's Bay), Harrison's Lighthouse and South Point (Fig. 1).

Little Bay (Figs. 2A, 3):

The Little Bay station was similar to the east coast station described by Lewis (1960). This station was exposed to the prevailing north-easterly and easterly winds, (Sailing Directions, 1948), and was subjected to heavy wave action particularly during the winter months. The area consisted of a seaward platform, approximately at mean sea level, varying in width from 5 to over 30 meters and 200 meters long. The platform rises to meet the landward limestone cliffs by a series of more or less sudden elevations. There were boulders and debris along the base of the cliffs. The whole area

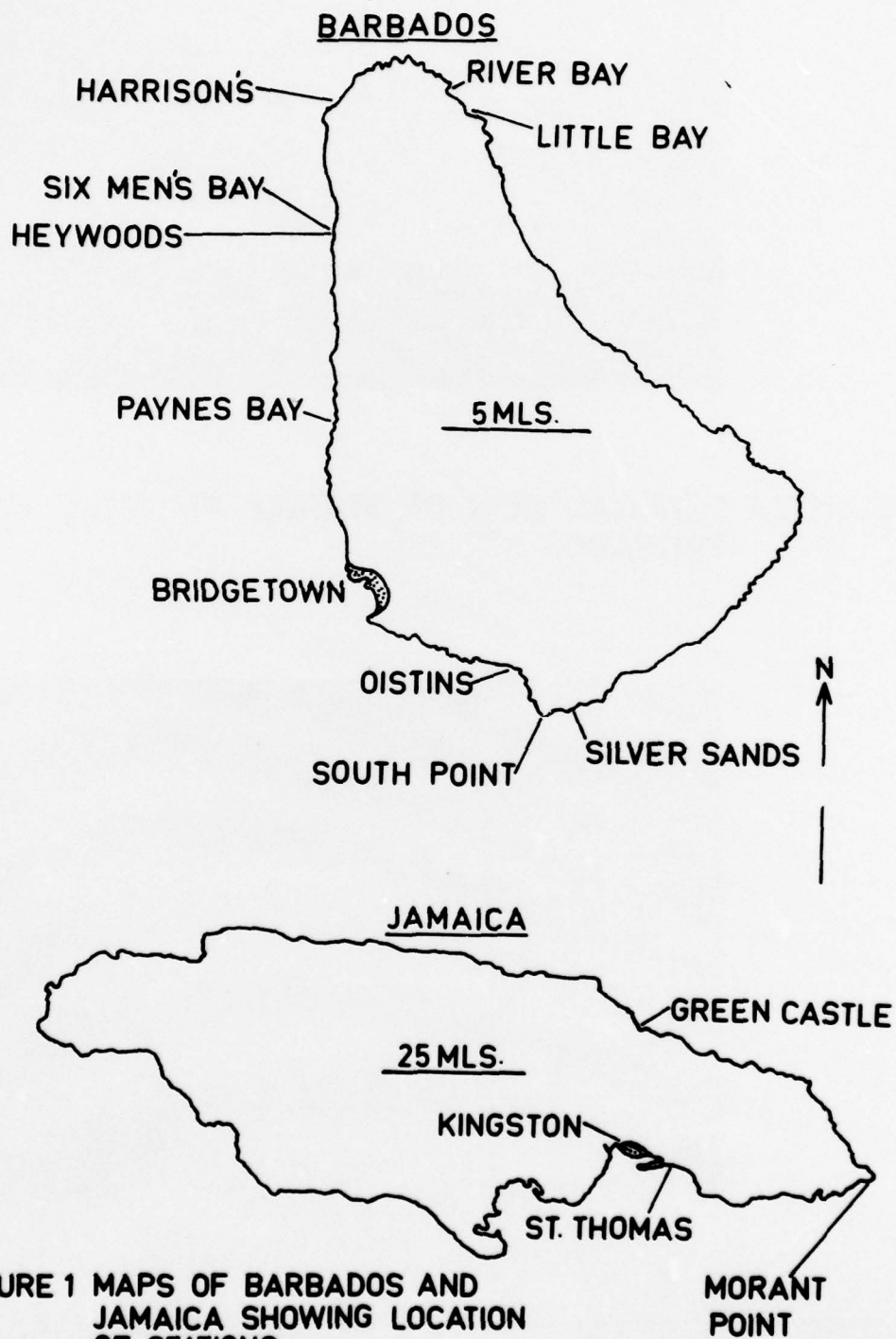


FIGURE 1 MAPS OF BARBADOS AND JAMAICA SHOWING LOCATION OF STATIONS.

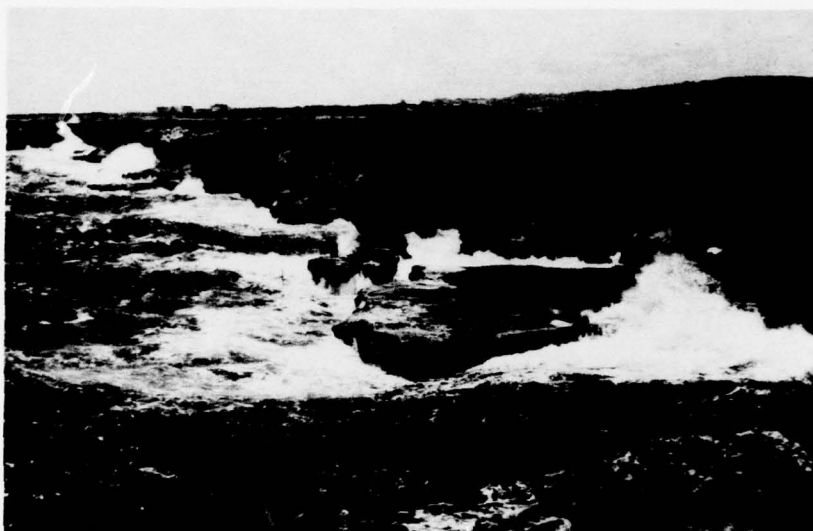
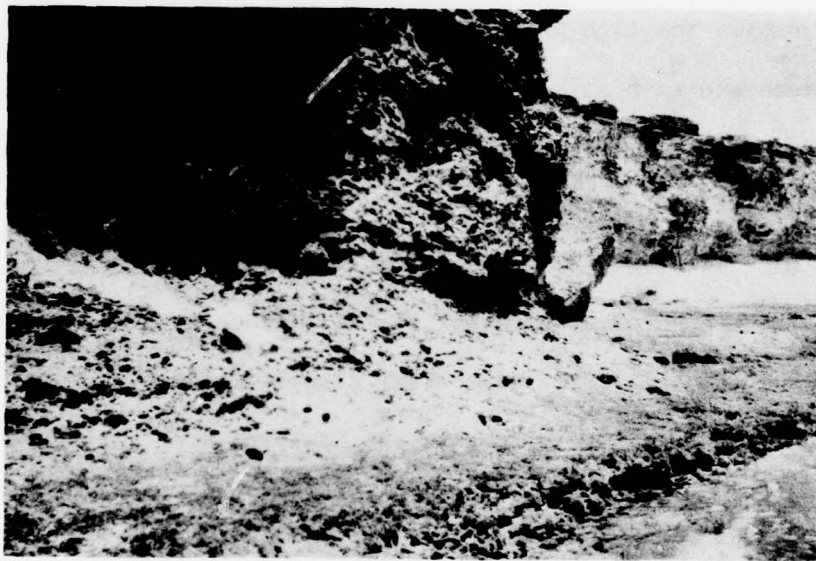


FIGURE 2A GENERAL VIEW OF STATION AT LITTLE BAY,
BARBADOS.



FIGURE 2B GENERAL VIEW OF STATION AT HARRISON'S
LIGHT, BARBADOS.



**FIGURE 3 DETAILED VIEW OF STATION AT LITTLE BAY
BARBADOS, SHOWING ZONATION.**

was covered by depressions and crevices, affording protection from wave action. The vertical profile contained the six faunal zones described by Lewis (1960). The six mollusc species investigated were found in the mid and upper intertidal regions (the mid-littoral and supralittoral zones of Stephenson and Stephenson, 1949).

Heywood's Beach (Six Men's Bay):

This station is situated on the west coast of Barbados. It is not in the line of the prevailing winds and is subject to only moderate wave action. It consists of a low lying platform of beachrock, similar to that described by Lewis (1960), 35 meters long and 10 meters wide, which is fully exposed at low tide. The outer edge is deeply fissured and has a very irregular surface with many cracks and holes. The horizontal surface is also very rough and irregular. It supports a heavy growth of algae such as Cladophora, Centroceros, Ceramium, Neomeris, and Caulerpa spp. N. tessellata and the barnacle Tetraclita squamosa are the two dominant forms. The former tends to cluster in small depressions and reaches a density of 60 animals per square meter. N. versicolor and N. peloronta are entirely absent from the platform, while N. tessellata is abundant.

Harrison's Lighthouse (Fig. 2B):

The Harrison's Lighthouse station on the north-west of the island was largely protected from the prevailing winds. As a result, rough wave conditions occurred infrequently and these were usually long period waves from storm conditions originating some distance from the island. This station was similar to Little Bay except that it was on a much smaller vertical scale. The area under study extended

for about 200 meters along the shore. The platform at mean sea level varied in width from less than a meter to a maximum of 3 meters.

The limestone cliff, landward of the platform, reached a maximum height of 4 meters. From the top of this cliff, the land sloped upwards by a steep escarpment to a height of about 100 feet. The zonation here was of the same type as that at Little Bay but due to generally reduced wave action it was vertically compressed. There were also many surface rock depressions and crevices here to afford protection to the fauna.

South Point:

The station at South Point received even less wave action than Harrison's Lighthouse because of protection from the prevailing winds. There was a fringing reef which dissipated most of the energy of the sea swells. The land sloped gently to the sea with a maximum height of 1.5 meters at the seaward escarpment and an average height of about 0.5 meters. The land vegetation came to within an average distance of 4 to 5 meters of the water's edge. This area was greatly eroded and was covered by crevices and deep holes. The typical zonation previously mentioned was unrecognizable for the most part due to the absence or narrowness of some of the zones.

FIELD STATIONS - JAMAICA

Three field stations were selected for study in Jamaica at Morant Point Lighthouse, Green Castle and St. Thomas (see Fig. 1).

Morant Point Lighthouse (Fig. 4A):

This station is situated at the extreme eastern end of the island where it is fully exposed to prevailing north-easterly winds and ocean swell. The rocky shore slopes gently with only a difference of about one meter between the top of the shore and the seaward edge. The width of the shore varies between 20 to 30 meters and the zones proposed by Stephenson and Stephenson (1949) in Florida could be recognised. The gradual slope of the shore thus extends the intertidal region over a relatively large area. The three species of Merita are all abundant in this area.

Green Castle (Fig. 4B):

This site is situated on the north-east coast of Jamaica and the coastline consists of a series of small cliffs about 20 feet in height fully exposed to wind and waves. Since the shore is steep the intertidal zones are narrow and this limits the areas available to the intertidal fauna.

The tops of the cliffs are very rough and pitted and, except on calm days, are moist from sea spray. Large numbers of T. muricatus are found on the tops of these cliffs, while N. tuberculata and L. ziczac are more common in the lower regions which receive more moisture. The intertidal region at this site can also be subdivided into zones suggested by Stephenson and Stephenson (1949). There is a large supralittoral fringe which could be subdivided into white, grey and black zones with a small midlittoral zone at the base of the cliff.



FIGURE 4A GENERAL VIEW OF STATION AT MORANT POINT, JAMAICA.



FIGURE 4B GENERAL VIEW OF STATION AT GREEN CASTLE, JAMAICA.

St. Thomas:

This site is on the south coast and consists of a series of small cliffs and outcrops of rocks varying in height from 3 to 10 feet. It is not an exposed region and is situated in a relatively dry part of the island. Some of the rock outcrops receive a considerable amount of splash on windy days. Large populations of L. ziczac and N. tuberculata are found here. T. muricatus is found in large numbers on the small cliffs in the supralittoral zone. The grey and white zones are wide; there is a small black zone at the base of the cliff and a very narrow upper yellow zone below this. The latter zone is often covered with sand.

ENVIRONMENTAL FACTORS

Daily weather records were obtained from representative stations in both Barbados and Jamaica over more than a two year period. At Little Bay, North Point and at Harrison's Point in Barbados, weather stations were set up to record daily maximum and minimum temperatures, daily rainfall, relative humidity and wind. In addition, temperature observations were made in the immediate environment of the animals themselves, in order that the relationships between microclimates and general site conditions might be assessed. Comparison of site conditions can also be compared with data available from the Government meteorological station at Seawell airport on the south coast of Barbados.

Similarly, records of daily temperature, rainfall, relative humidity and wind were obtained from stations at Green Castle and

Morant Point in Jamaica. Detailed meteorological data were available from November 1965 to July 1967 for Morant Point Lighthouse and were supplied by the West Indies Meteorological service at Palisadoes. Daily readings of minimum and maximum air temperatures were available together with readings taken at three hour intervals of wind speed, wind direction, cloud, relative humidity, barometric pressure and dew point. A station was set up at Green Castle in July 1966 and daily readings of rainfall, temperature and relative humidity were recorded. Wind measurements were taken for one month.

Microclimatic data were taken at the different sites, as in Barbados, whenever they were visited from April 1966. Temperatures were taken with a thermistor of different parts of the rock, such as the rock surface, holes, crevices and rock pools. Wind speed measurements were taken with a hand anemometer.

Mean monthly observations from Barbados are shown in Figures 5-11. Mean monthly minimum temperatures varied between 22.5° and 27.0°C at both North Point and Little Bay (Fig. 7). Maximum temperatures varied between 27.5° and 31°C with the highest temperatures occurring at the Harrison's Point station. Temperatures at both sites were thus similar to the temperatures measured at Seawell airport (Fig. 5).

The highest rainfall was recorded at each station in November of each year (Fig. 8). Rainfall was lowest at the North Point station and highest at Little Bay. The monthly rainfall totals at each of the three stations were, however, considerably less than the monthly amounts of rainfall at Seawell airport (Fig. 6).

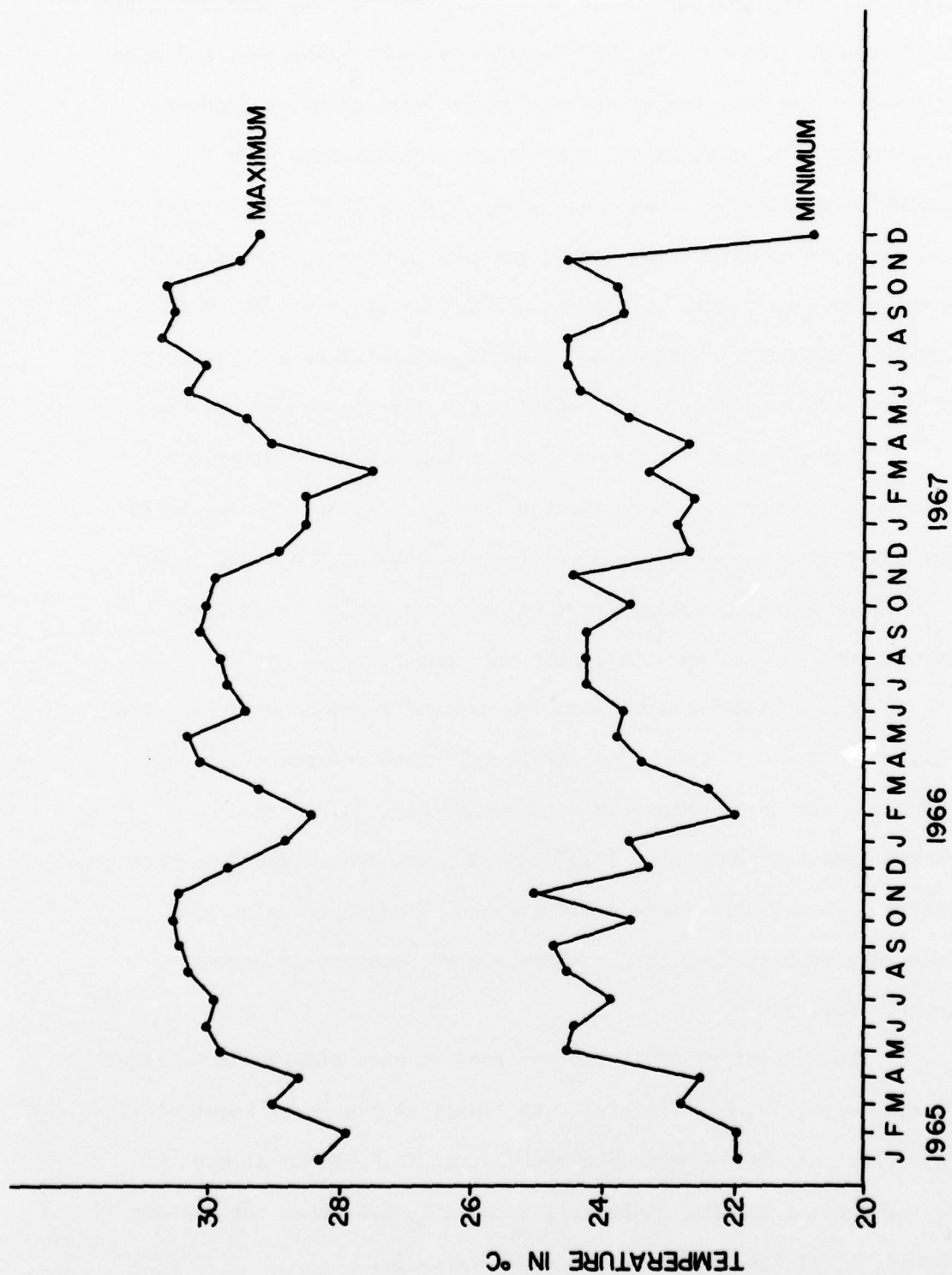


FIGURE 5 MEAN MONTHLY TEMPERATURES, SEAWELL AIRPORT, BARBADOS.

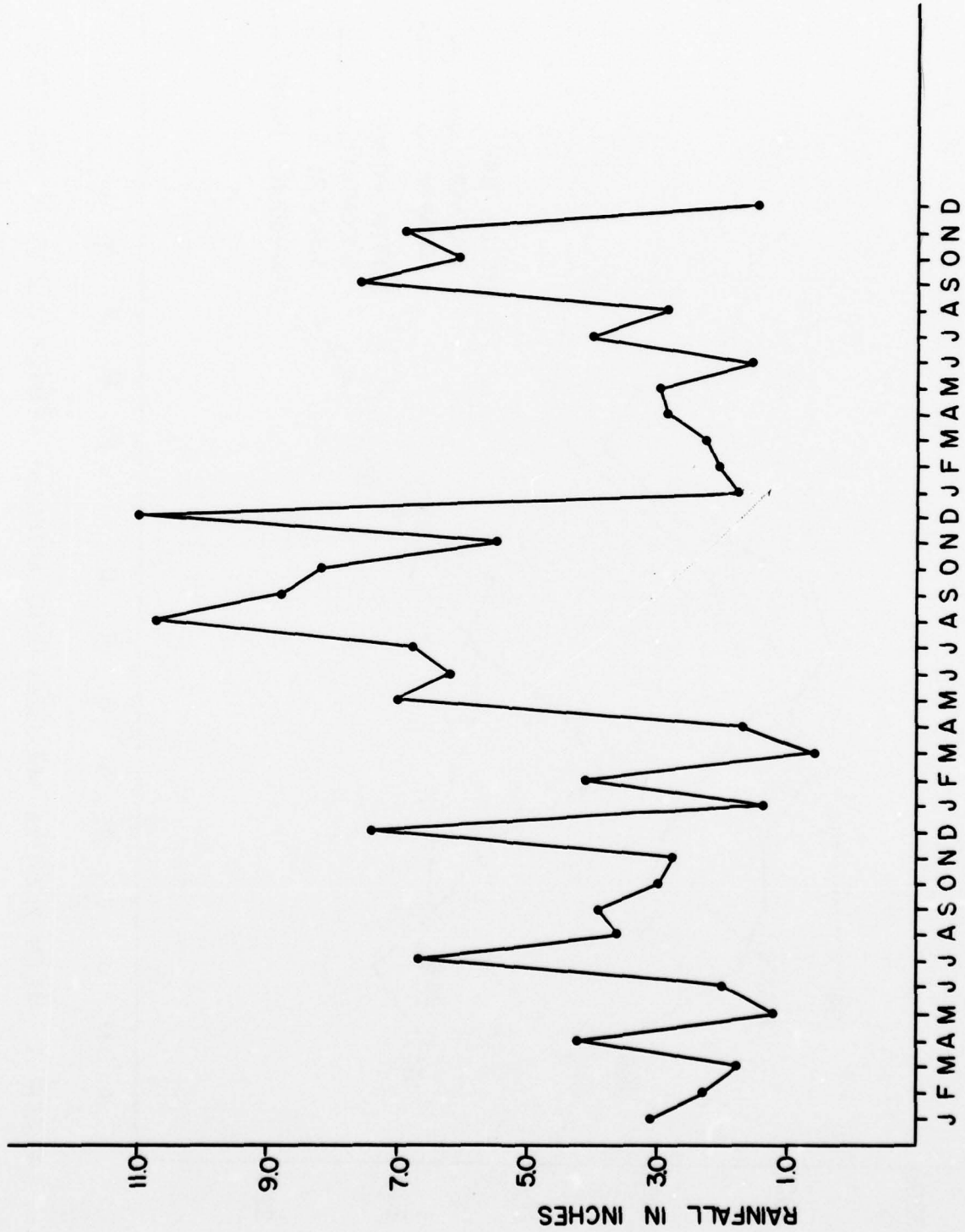


FIGURE 6 MEAN MONTHLY RAINFALL, SEAWELL AIRPORT, BARBADOS.

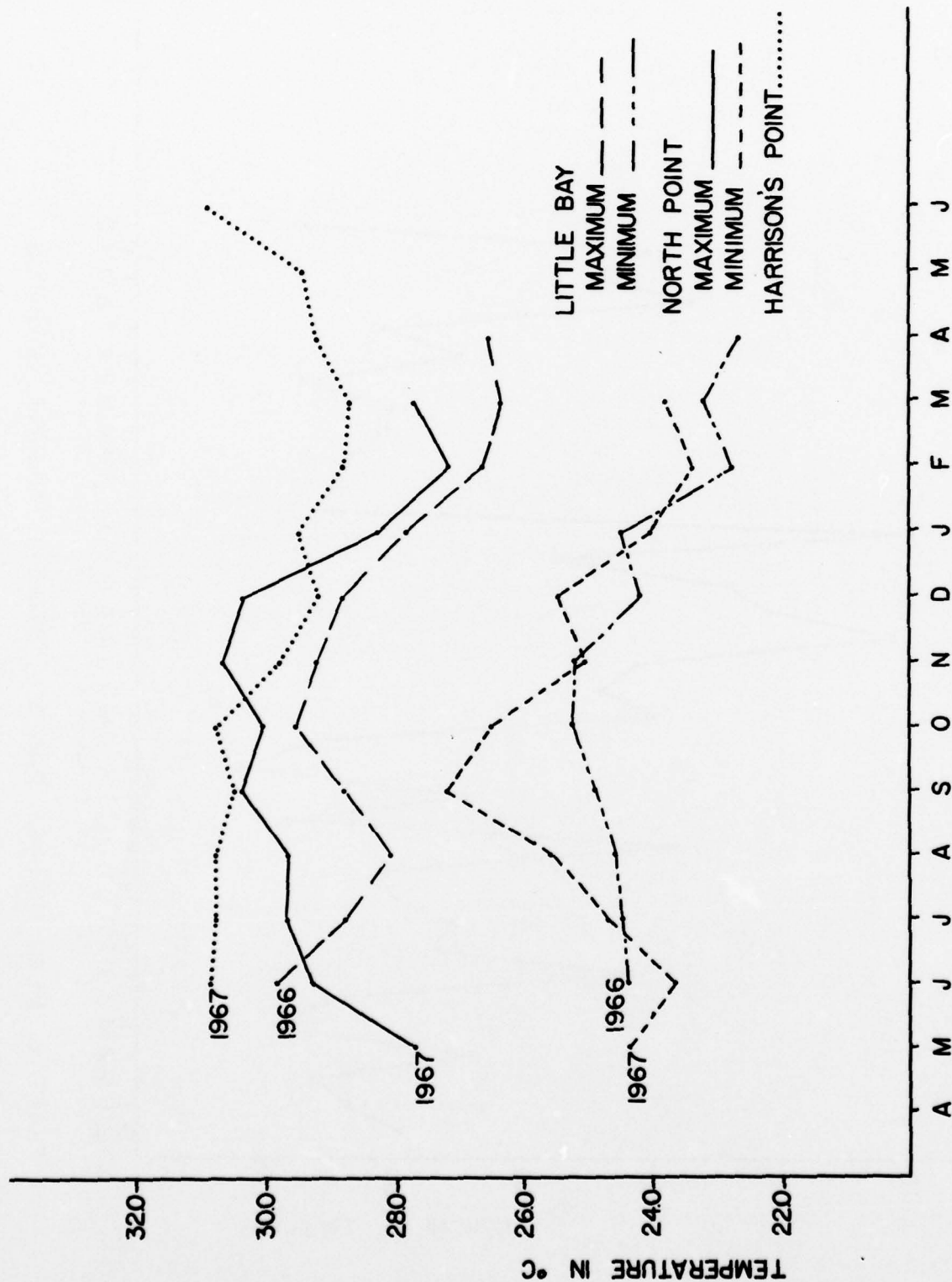


FIGURE 7 MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURES IN BARBADOS.

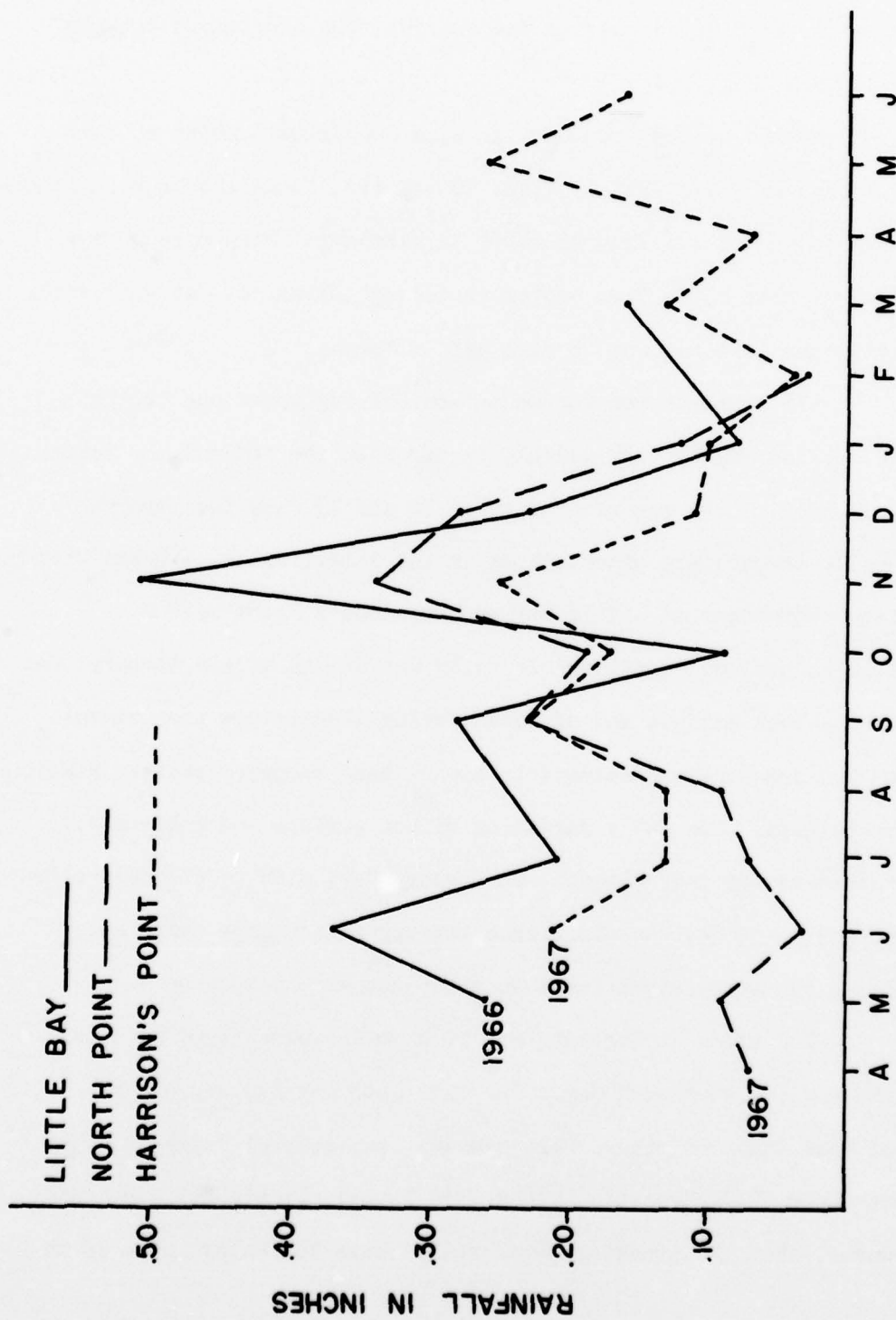


FIGURE 8 MEAN MONTHLY RAINFALL IN BARBADOS.

The mean monthly relative humidities from both North Point and Harrison's Point were both low in May to August of 1967, but during the rest of the period the observations fluctuated between 88% and 98% (Fig. 9).

Marked seasonal changes in wind speeds were noted at both Little Bay and North Point (Figs. 10 and 11). Wind speeds were highest in May to August and from December to February. Wind speeds were lowest at both sites from September through November. At Harrison's Point winds were highest in June and in March.

Air temperatures in the intertidal region, close to the rock surface may be considerably higher than the ambient air temperatures (Lewis 1963). The curves of figures 12 and 13 show the results of daily temperature observations in the intertidal zone taken with a fine thermistor at Little Bay and Harrison's Point over a prolonged period. Considerable daily variations of air temperature close to rock surface and of rock crevice temperature are evident and are frequently considerably higher than recorded weather station temperatures. The daily variation of sea surface and ambient air temperature was only slight. On a sunny day, with no clouds, moderate wind and low tide, the difference between ambient air temperature and the air temperature close to the rocks was as much as 10°C .

The tides at Barbados are of a semi-diurnal type with two highs and two lows each day. One tide each day has a greater amplitude than the other. The average semi-diurnal range is about one meter (U.S. Geodetic Survey Tide Tables, 1968). It was found, however, that the breaking waves could raise the water level up to

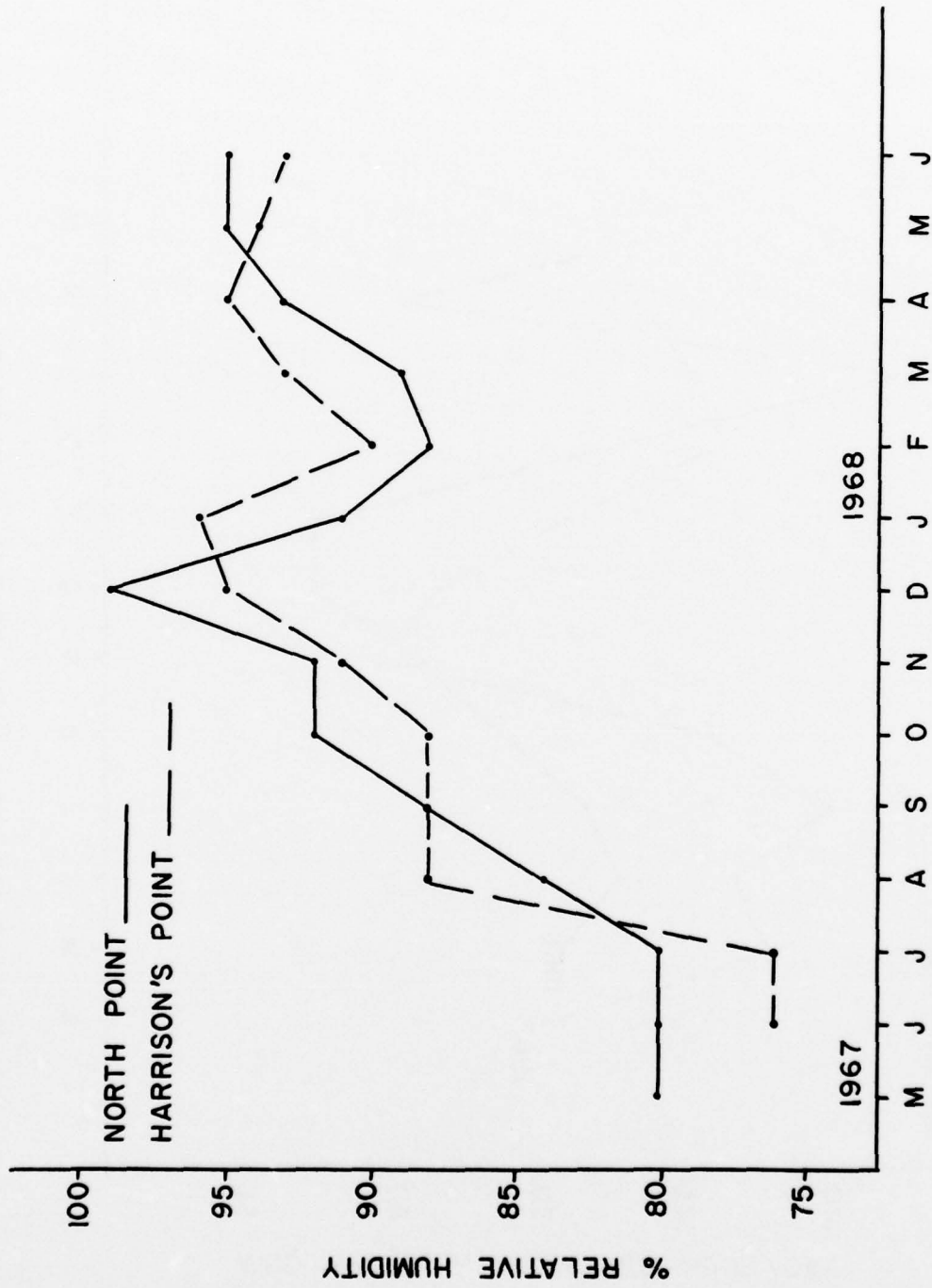


FIGURE 9 MEAN MONTHLY RELATIVE HUMIDITIES IN BARBADOS.

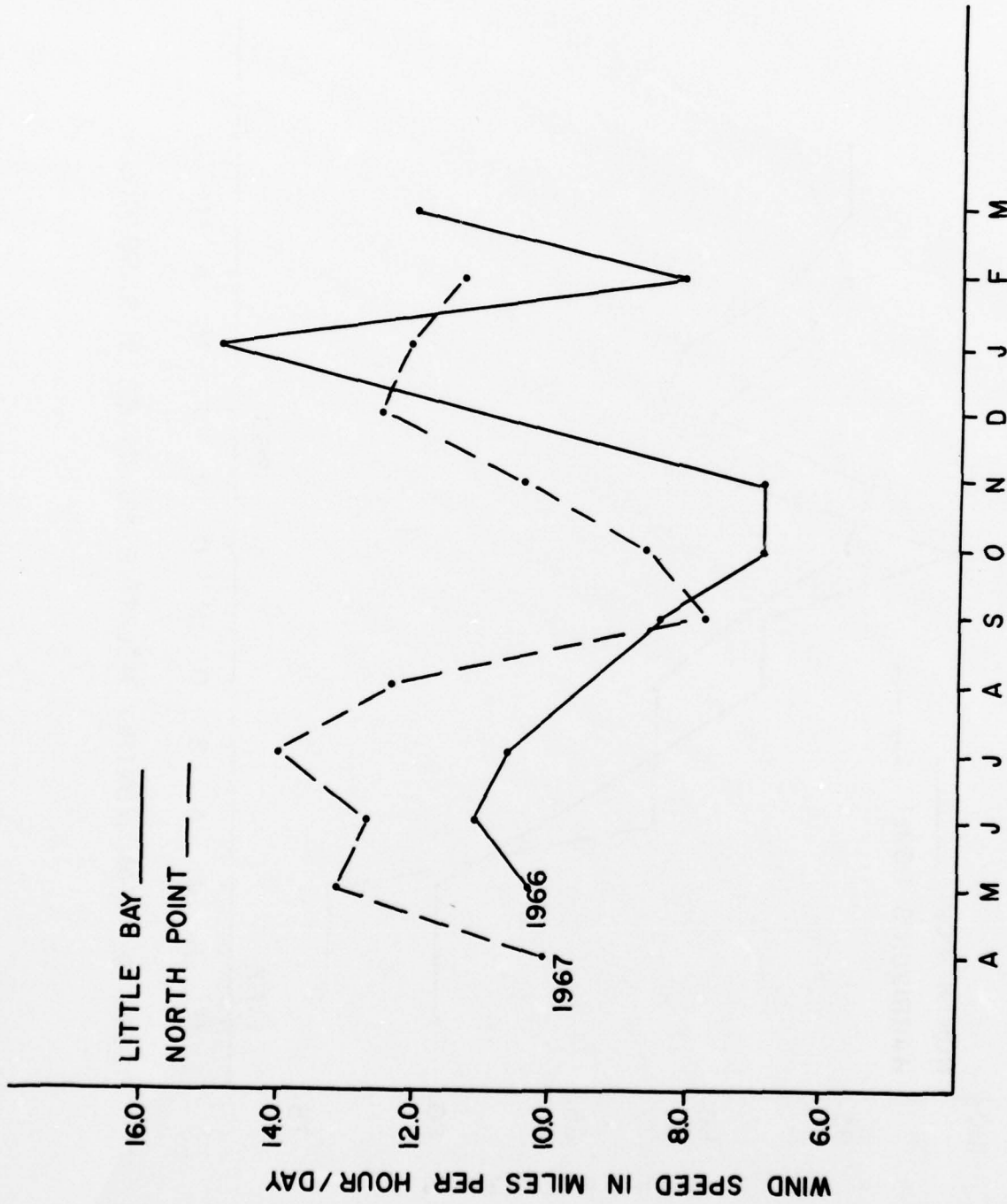


FIGURE 10 MEAN MONTHLY WIND SPEEDS IN BARBADOS.

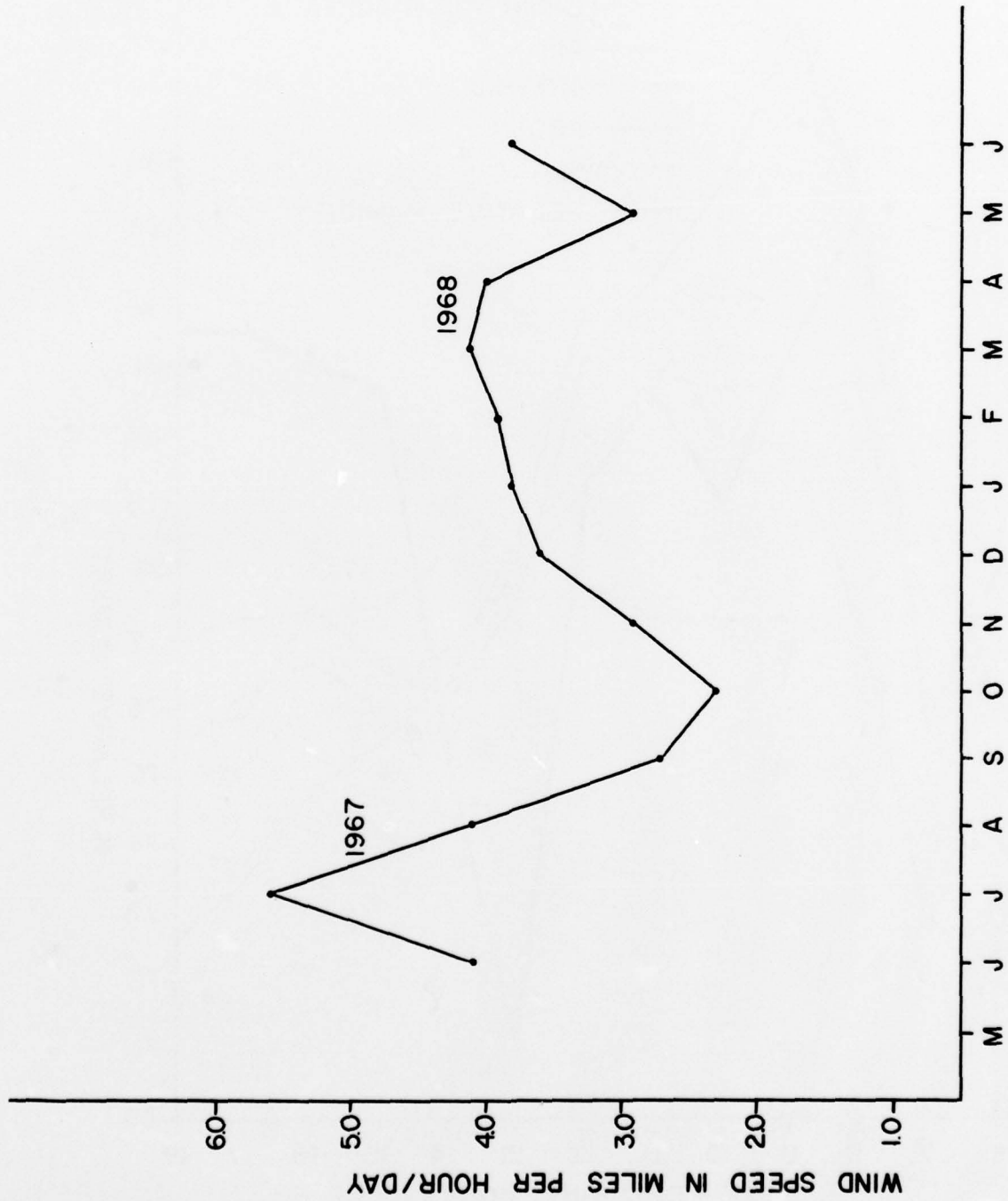


FIGURE II MEAN MONTHLY WIND SPEEDS IN BARBADOS, HARRISON'S POINT.

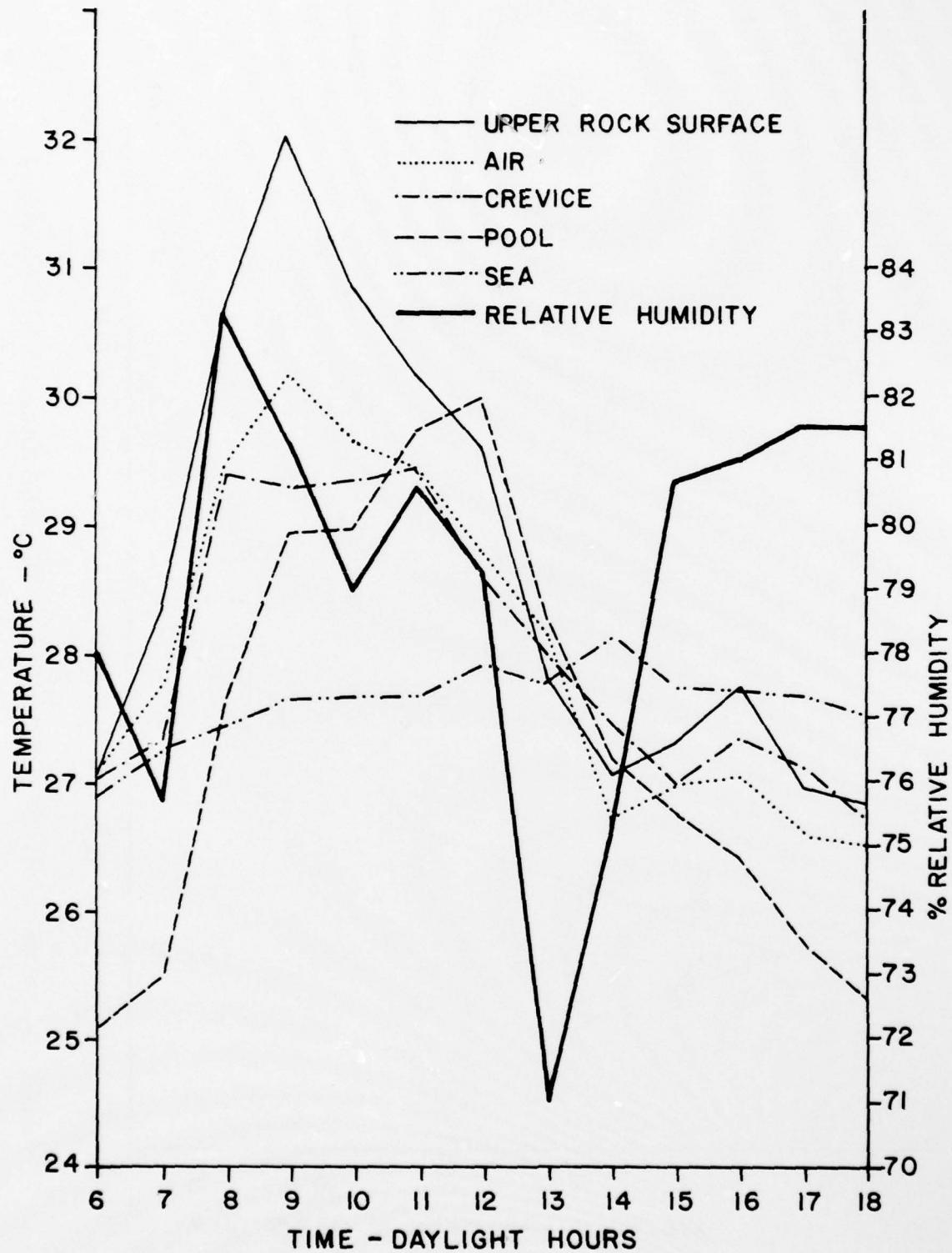


FIGURE 12 MICROCLIMATE DATA GRAPHS FROM
LITTLE BAY, BARBADOS.

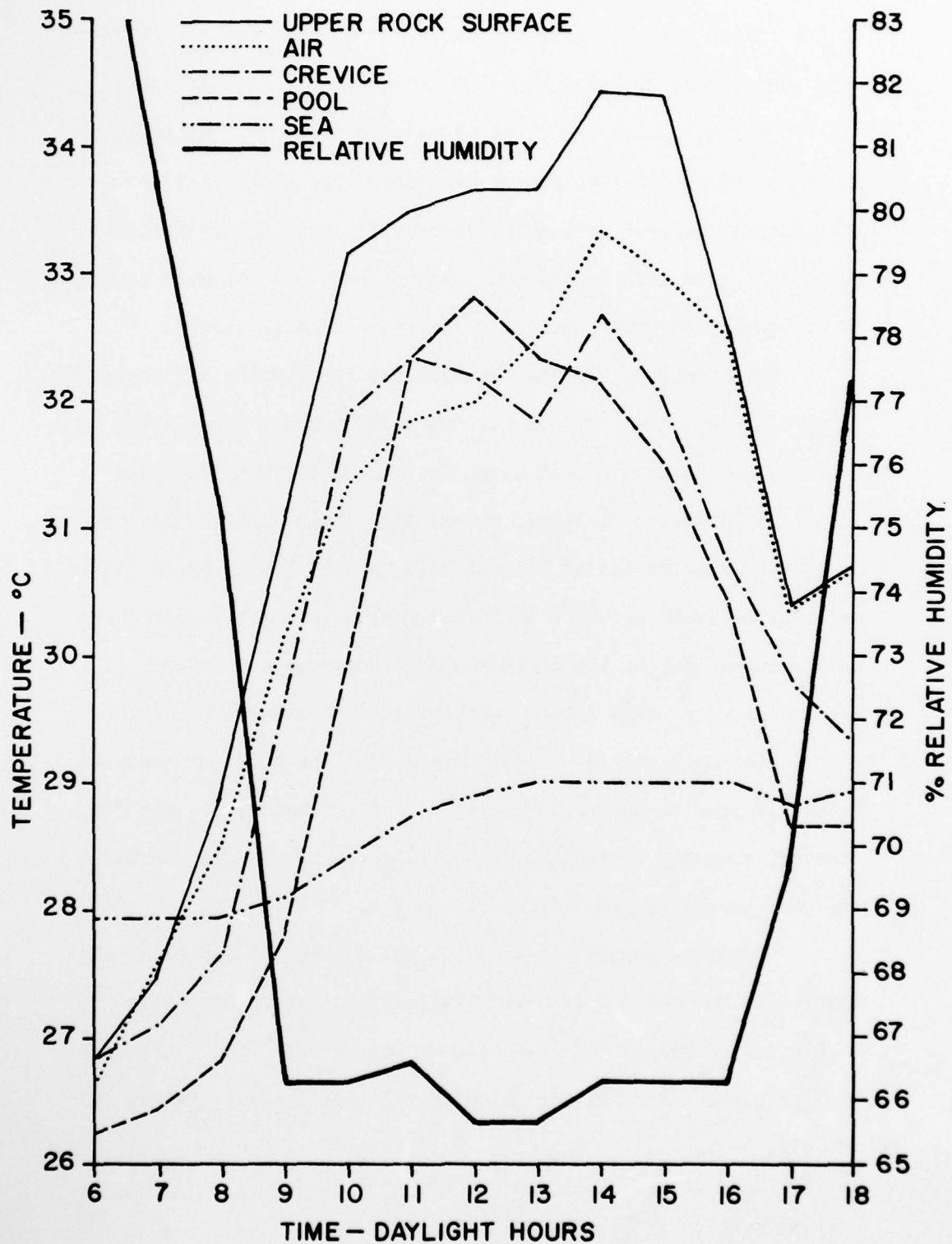


FIGURE 13 MICROCLIMATE DATA GRAPHS FROM
HARRISON'S LIGHTHOUSE, BARBADOS.

2 meters above the level predicted in the tide tables. The height of the splash zone is, however, difficult to estimate, as it varies with the kind of weather and the topography at any given area.

There is a marked contrast between the wave amplitudes on the east and the west coasts of Barbados. The east coast is continuously subject to heavier wave-action than the west coast. Reproduction of wave records on both the east and the west coasts of Barbados have been previously reported by Lewis (1960).

Mean monthly weather observations for Jamaica are shown in figures 14-20. Mean monthly maximum daily temperatures varied between 27.0° and 30.4°C at Green Castle and between 27.8° and 31.5°C at Morant Point (Figs. 14 and 15). Mean monthly minimum daily temperatures varied between 18.2° and 22.4°C at Green Castle and between 19.0° and 25°C at Morant Point. Highest temperatures were recorded during the period June to November and lowest temperatures occurred during the winter from December to May.

Rainfall was low in both areas with the greatest amounts being recorded in the period October to December. There was not, however, a marked inequality of distribution of rainfall throughout the year in either area (Figs. 16 and 17).

Relative humidities were highest during the winter months and ranged between 78% at Green Castle in August of 1966 to a high value of 92% at the same site in October of 1967. There was thus no marked seasonal variation in relative humidity (Figs. 18 and 19).

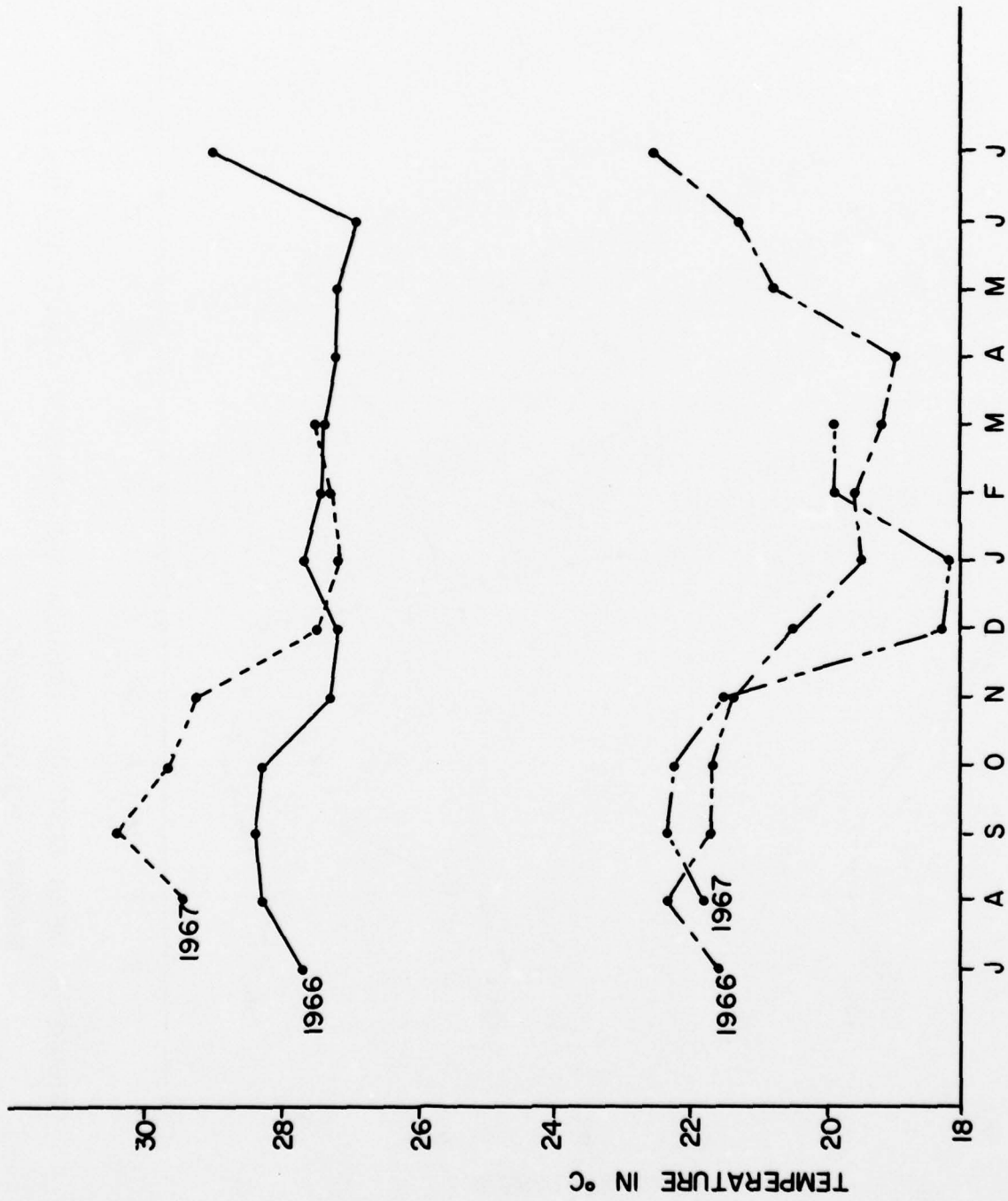


FIGURE 14 MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURES,
GREEN CASTLE, JAMAICA.

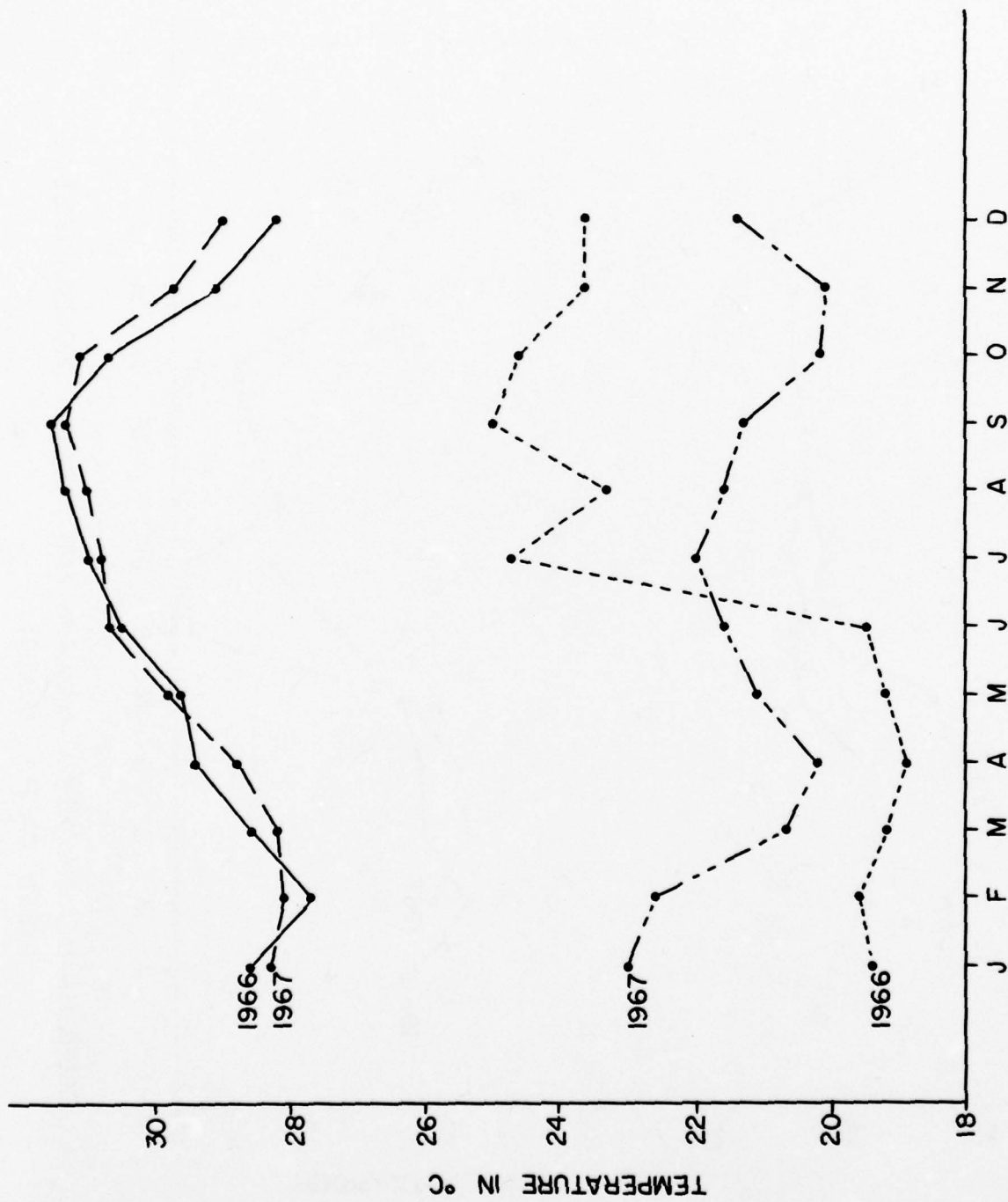


FIGURE 15 MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURES,
MORANT POINT, JAMAICA.

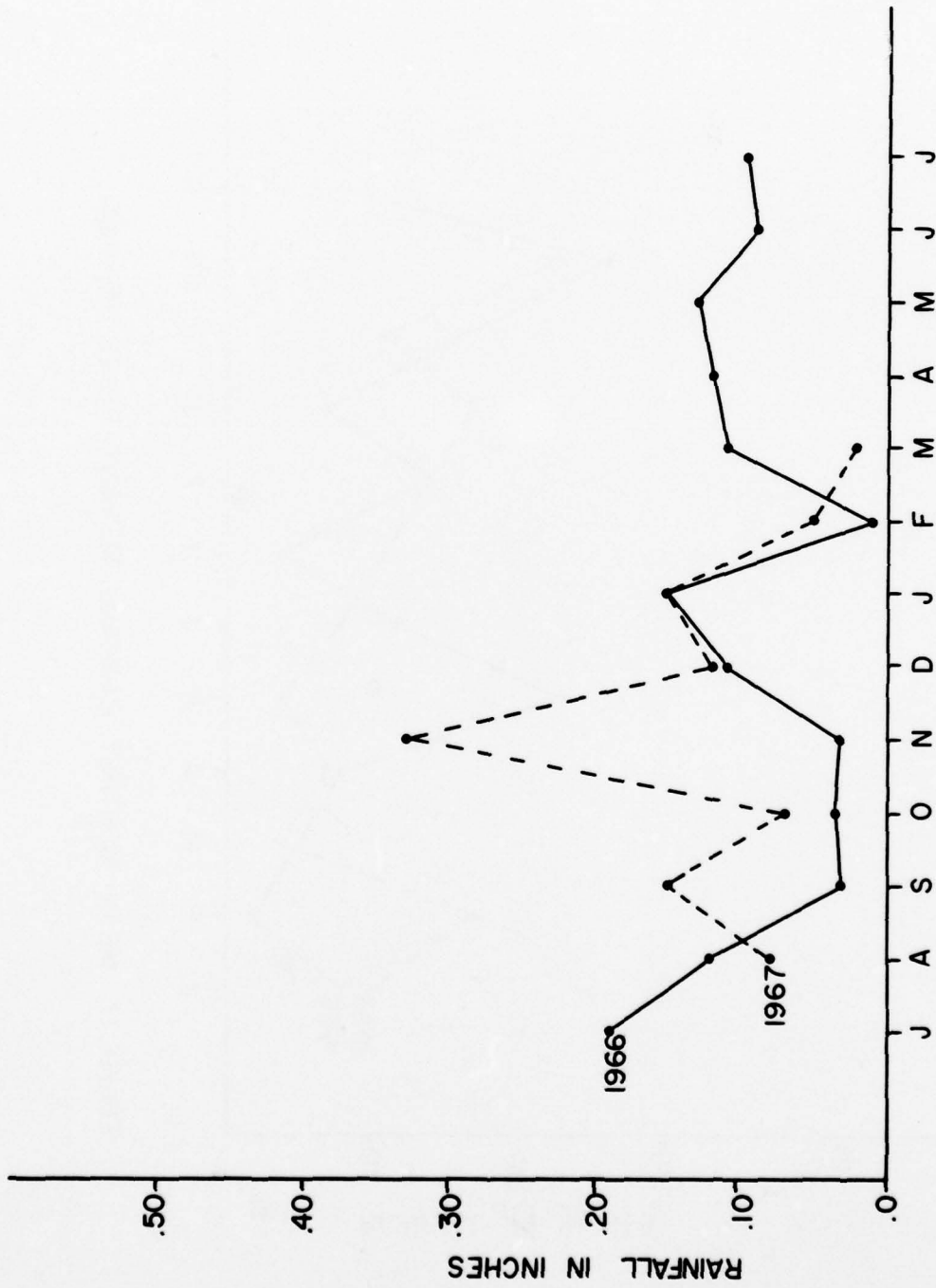


FIGURE 16 MEAN MONTHLY RAINFALL, GREEN CASTLE, JAMAICA.

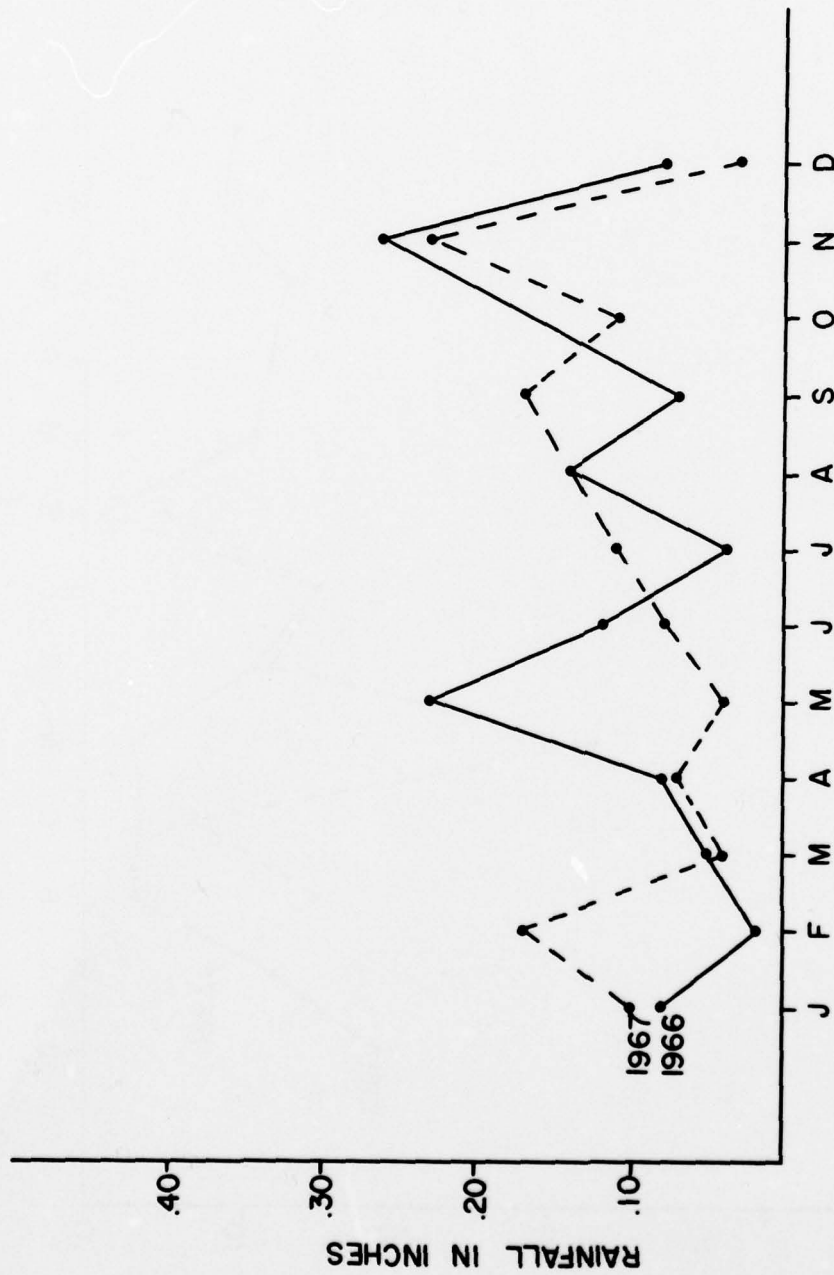


FIGURE 17 MEAN MONTHLY RAINFALL, MORANT POINT, JAMAICA.

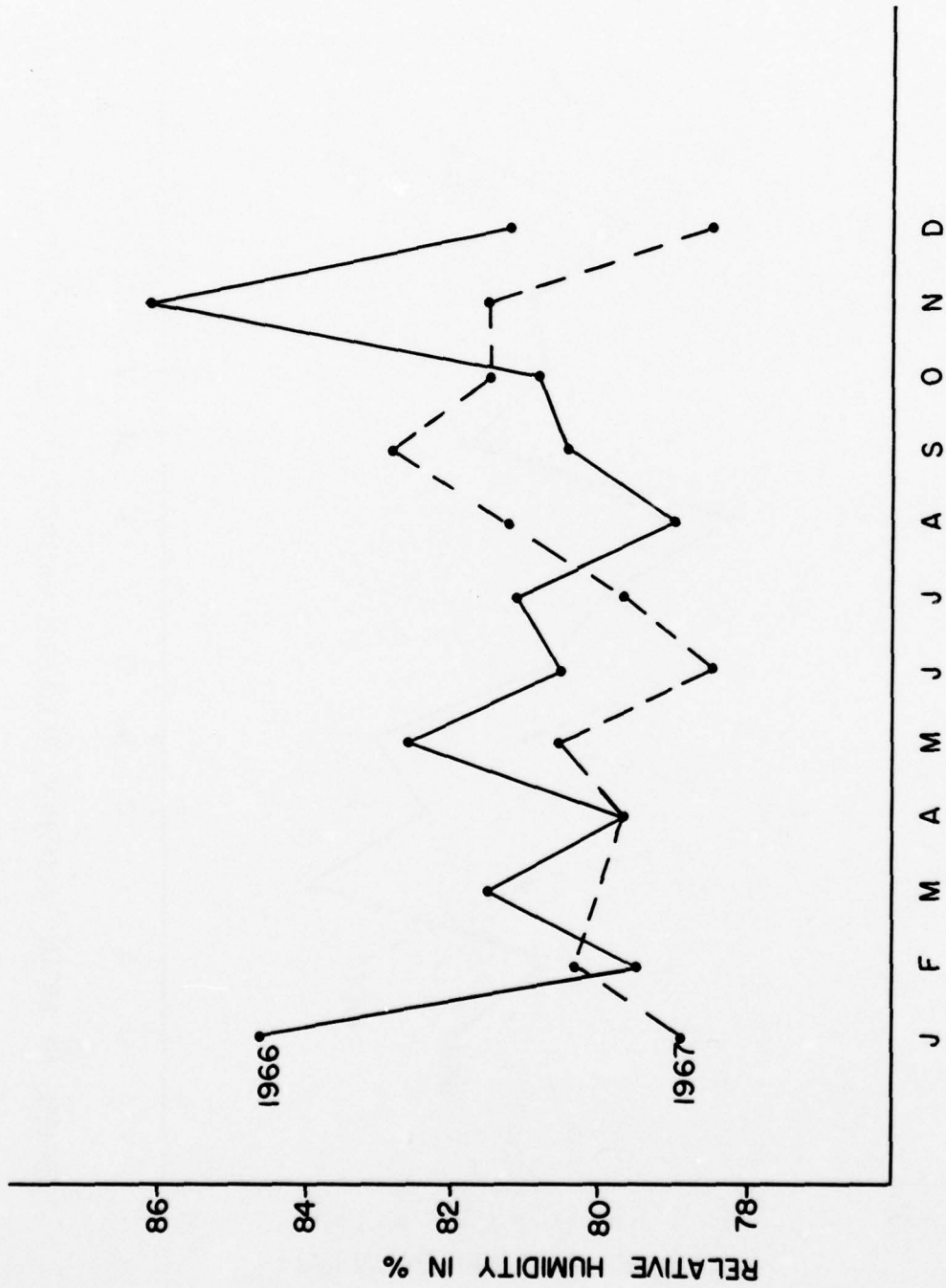


FIGURE 18 MEAN MONTHLY RELATIVE HUMIDITY, MORANT POINT, JAMAICA.

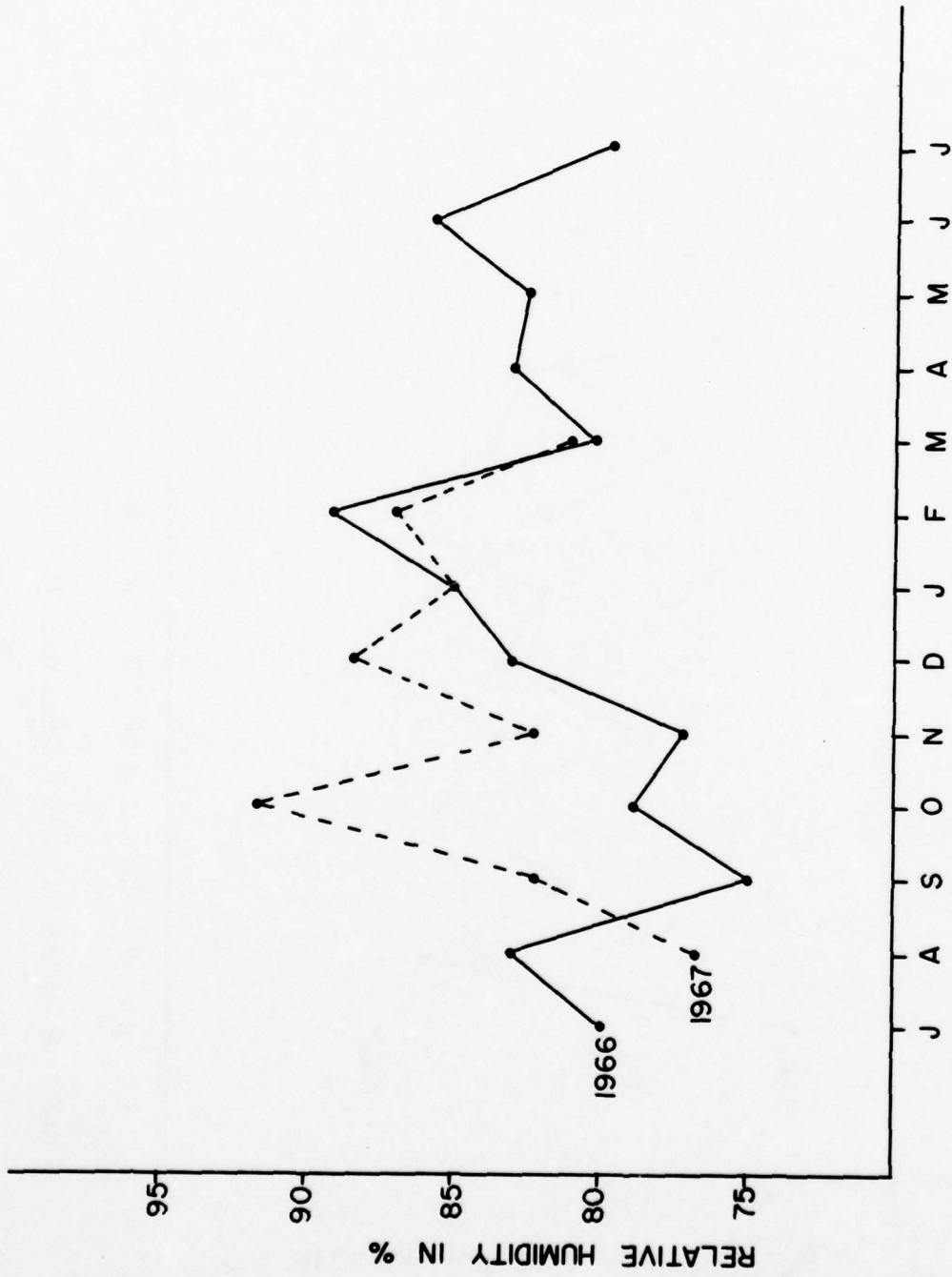


FIGURE 19 MEAN MONTHLY RELATIVE HUMIDITY, GREEN CASTLE, JAMAICA.

Wind speed showed a seasonal variation at Morant Point in both 1966 and 1967. Wind varied from highs of 8.4 and 10.6 miles per hour per day in January of 1967 and 1966 respectively, to lows of only 4.4 miles per hour per day in September and October of the same years. The seasonal pattern of variation was thus similar for both years (Fig. 20).

Sites at Green Castle on the north-east coast and at Morant Point Lighthouse at the extreme eastern tip of the island are both fully exposed to prevailing north-easterly winds, but the St. Thomas site on the south coast is in a more sheltered position.

The mean tidal range, based on the weekly extremes of low and high tides in Jamaica is small (about 24 cm). Tidal heights probably did not affect the environment at Green Castle on the north-east coast as much as the amount of spray and splash on the rocks which are most important in this area. When the sea was calm and there was very little wind, the tops of the cliffs were dry. A moderate easterly wind with choppy seas caused slight spray in exposed regions but none in the sheltered regions. A stronger easterly wind produced spray in both exposed and sheltered regions. At St. Thomas on the south coast a combination of high tide with a moderate south-easterly wind and rough sea produced a high splash zone. Wave action was thus considered to be most important at Morant Point Lighthouse.

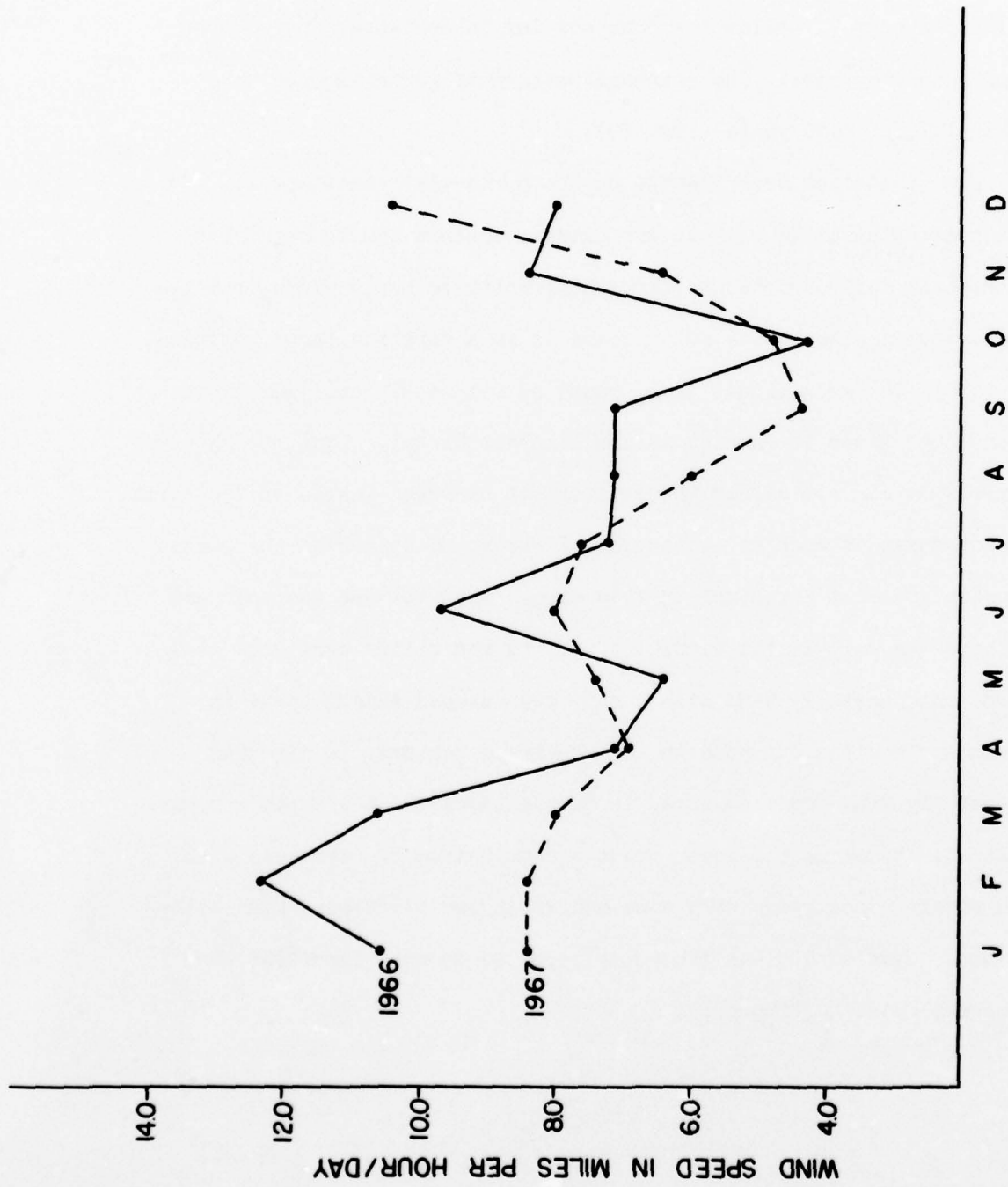


FIGURE 20 MEAN MONTHLY WIND SPEEDS, MORANT POINT, JAMAICA.

RESULTS AND DISCUSSION

A. SIZE FREQUENCY DISTRIBUTIONS

Frequency distribution histograms for the monthly random samples for three stations in Barbados are shown in Figs. 21-26. The results for Nodolittorina, Littorina and Tectarius suggests very slow rates of growth throughout the year. There is some evidence that two age classes are present in the population sample of Nodolittorina, but the increase in modal values from month to month is not regular and provides no accurate estimate of monthly growth. Animals of shell length between 2 and 3 mm in November of 1965 reached a size of 5 to 6 mm the following year. In the other two species there are only single modal values for each month but these are variable and it is not possible to detect a monthly increment from inspection of the histograms.

Both Nerita tessellata and Nerita versicolor have bimodal distributions. In Nerita tessellata an increase at Little Bay in the monthly modal value from about 7 mm in November of 1965 to 12 mm in June of 1966 is apparent. This represents a monthly growth increment of 0.7 mm. In September and October of 1966 the appearance of very small sizes of 2-6 mm indicates recruitment of young classes into the population, presumably from summer breeding activity.

In Nerita versicolor an increase of modal values from 7 mm in January of 1966 to 13 mm in November of the same year indicates an increase of growth of 6 mm in less than a year. This represents a monthly shell growth increment of more than 0.5 mm.

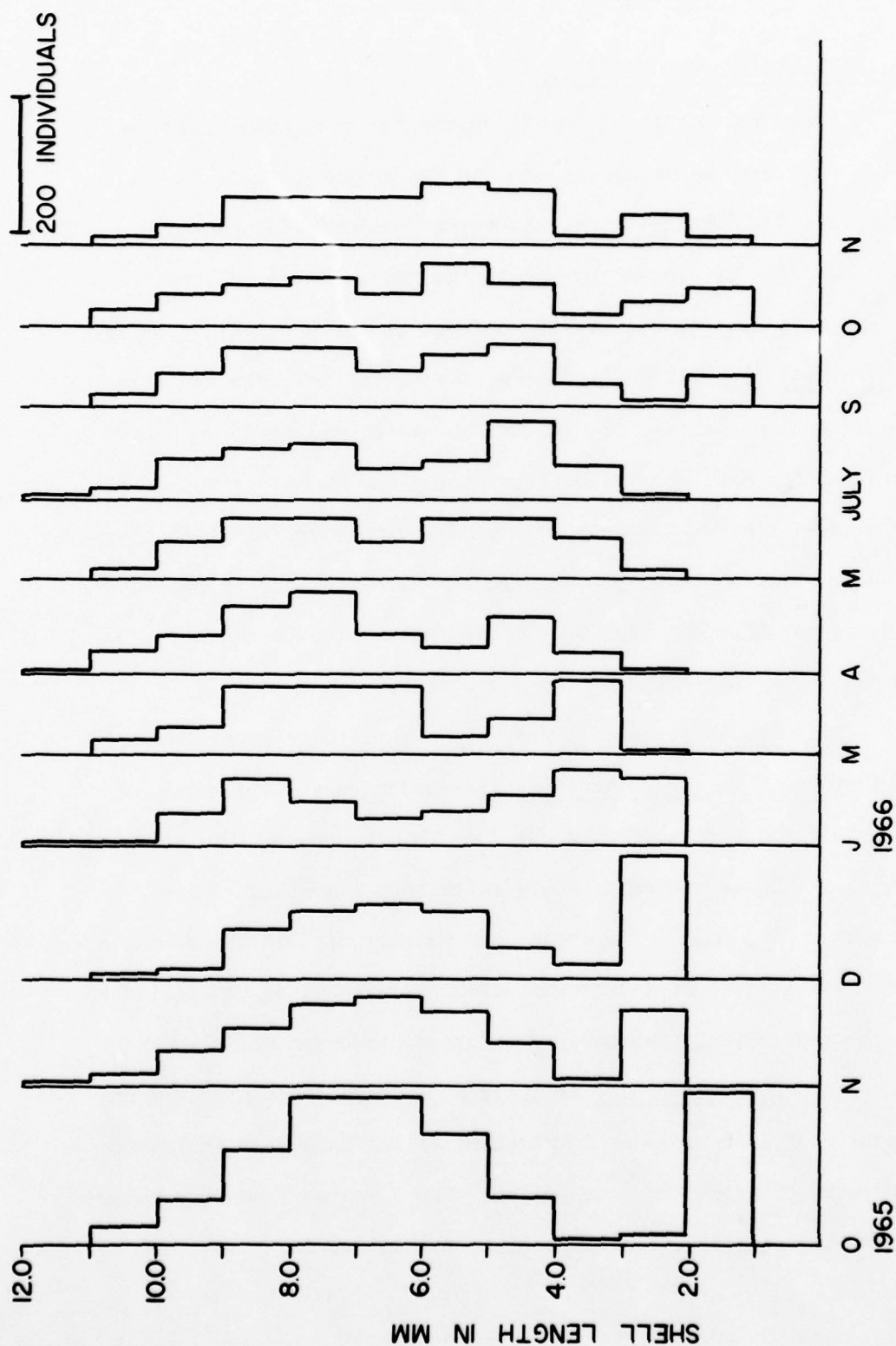


FIGURE 21 SIZE FREQUENCY DISTRIBUTIONS OF *NODOLITTORINA TUBERCULATA*,
PAYNES BAY, BARBADOS.

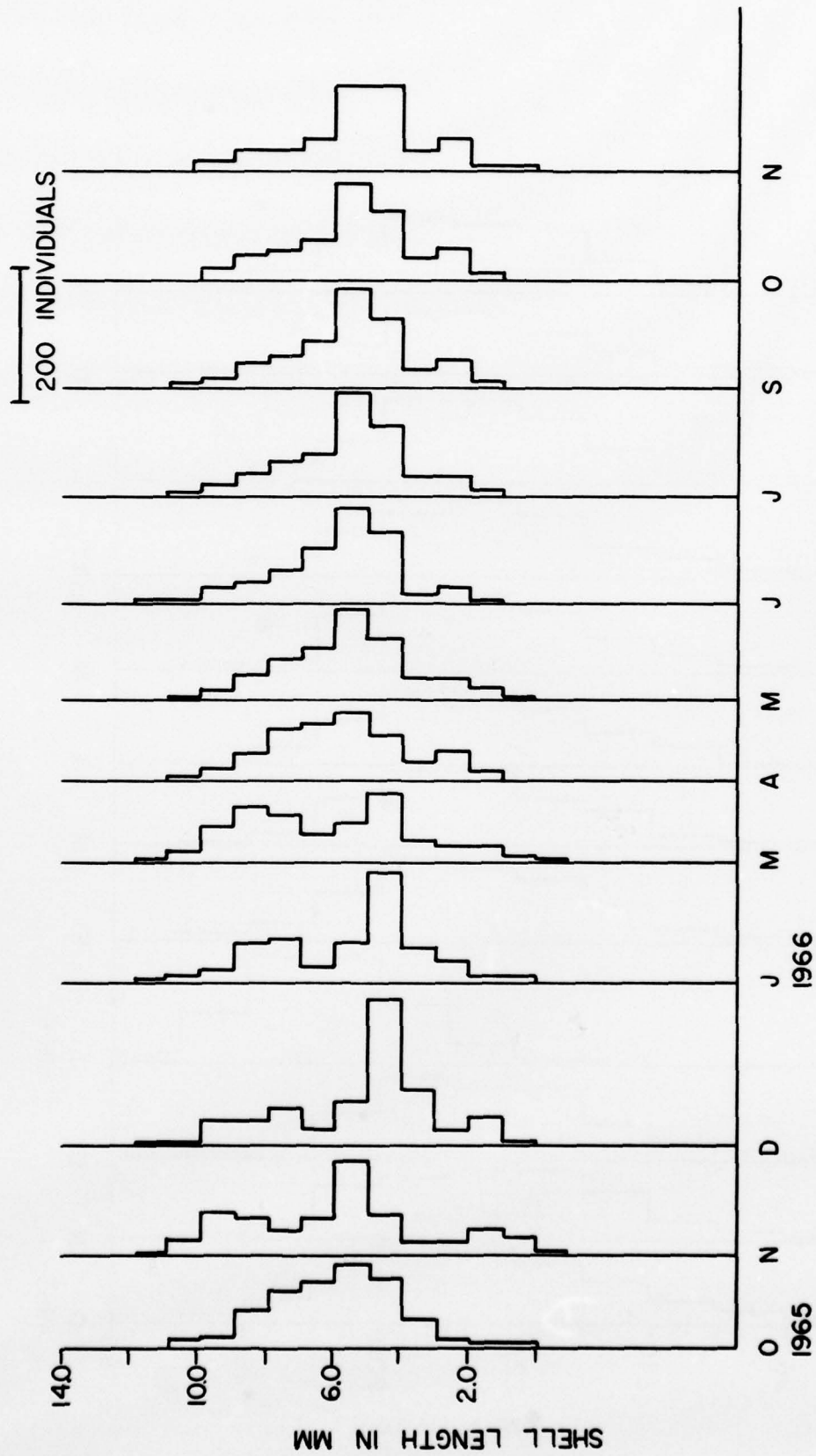


FIGURE 22 SIZE FREQUENCY DISTRIBUTIONS OF *LITTORINA ZICZAC*, PAYNES BAY, BARBADOS.

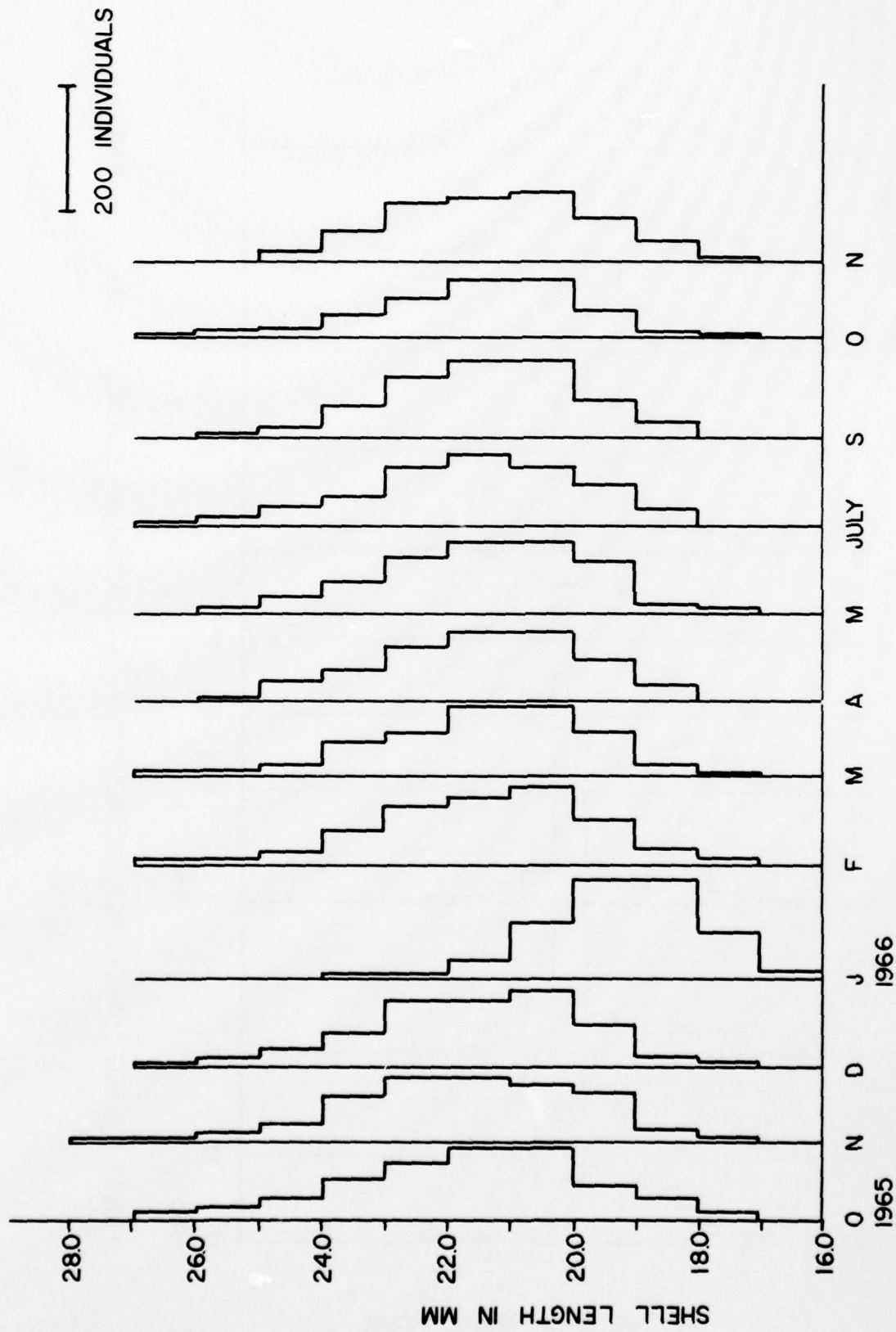


FIGURE 23 SIZE FREQUENCY DISTRIBUTIONS OF *TECTARIUS MURICATUS*, LITTLE BAY, BARBADOS.

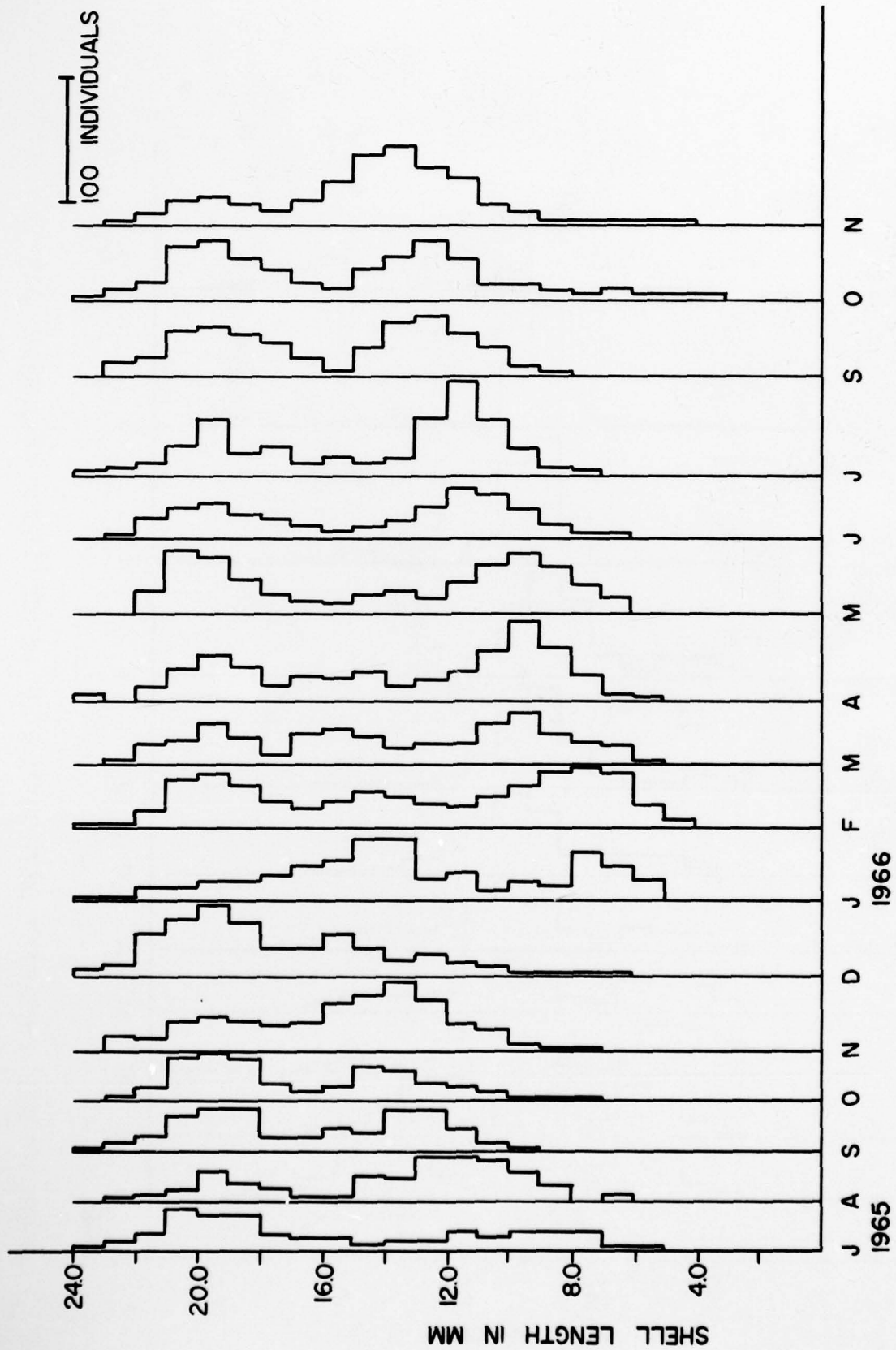


FIGURE 24 SIZE FREQUENCY DISTRIBUTIONS OF *NERITA VERSICOLOR*, LITTLE BAY, BARBADOS.

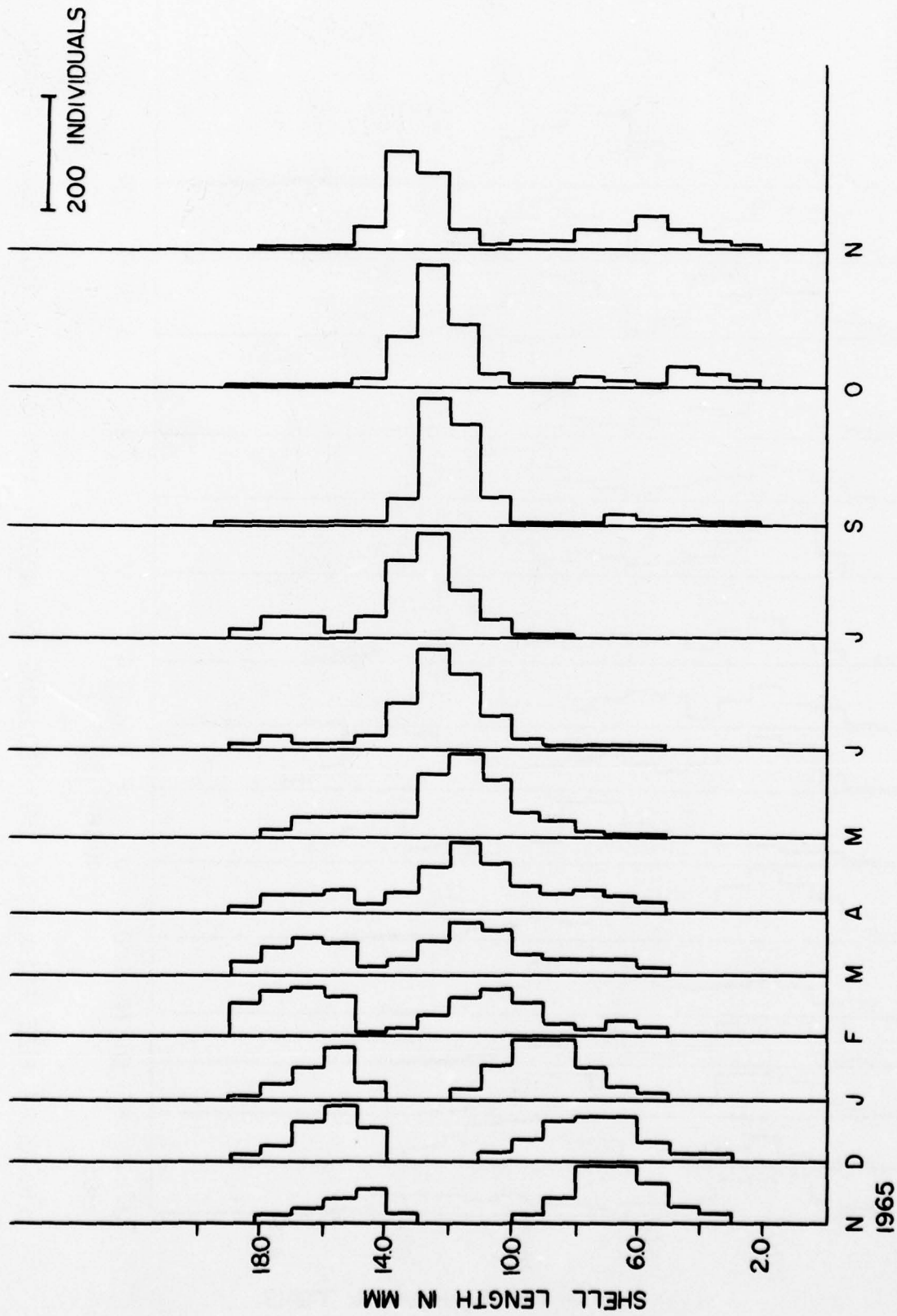


FIGURE 25 SIZE FREQUENCY DISTRIBUTIONS OF *NERITA TESSELLATA*, LITTLE BAY, BARBADOS.

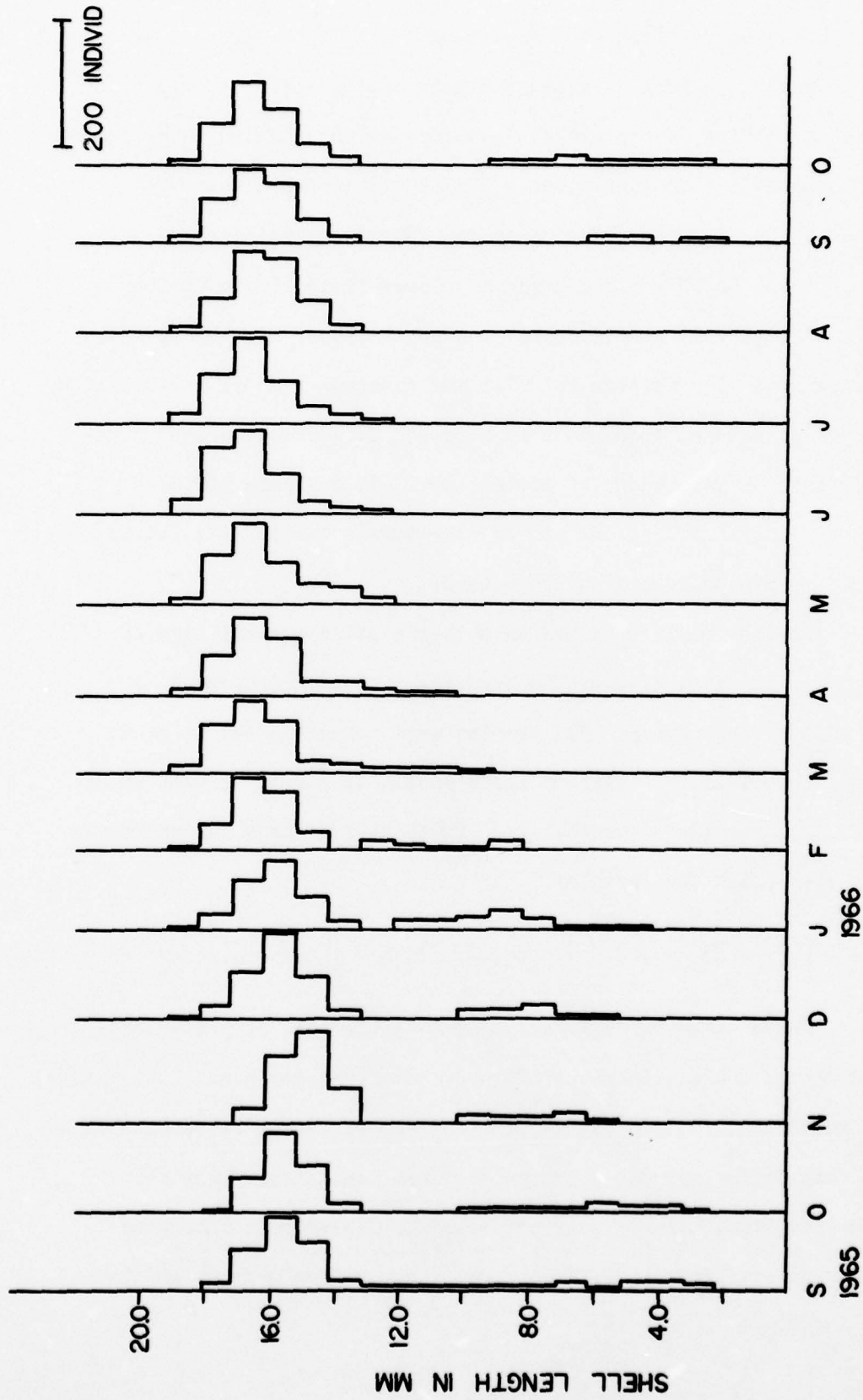


FIGURE 26 SIZE FREQUENCY DISTRIBUTIONS OF *NERITA TESSELLATA*, SIX MEN'S, BARBADOS.

Because the frequency distributions of both Nerita species were polymodal, a more detailed analysis of the various components of the population was undertaken by computer in order to determine growth rates of different sizes. FORTRAN IV programs were written to analyse the unimodal curves for mean, variance, SD, SE, ratio of mean to SD and the upper and lower fiducial limits for P.05 and P.01. All statistical terms are those of Stanley (1963). A program was also written to split the numerous bimodal distributions into their unimodal components by a method of successive approximations based on the theory of probability. In the case of the trimodal distributions, one of the side-modals was split visually and the remaining bimodal by computer.

All the means obtained were then plotted against time of collection in Figs. 27-29. The mean value of each component is included in the figures. All samples were not collected at exact monthly intervals but they are close enough to justify growth rates being designated in mm/month. The growth rate of each component was calculated using the formula:

$$Y = a + b (X - \bar{X}), \text{ where } Y = \text{size, } a = \bar{Y}, b = \text{growth increment, } X = \text{time}$$

Where there was a marked change in the rate of growth of a component of the population over a period of several months, the growth rate was calculated separately for that section. The regression lines were then fitted for each component of the population. For each regression line, a t-test was performed to determine whether the regression coefficient differed significantly from zero at limits P.05 and P.01.

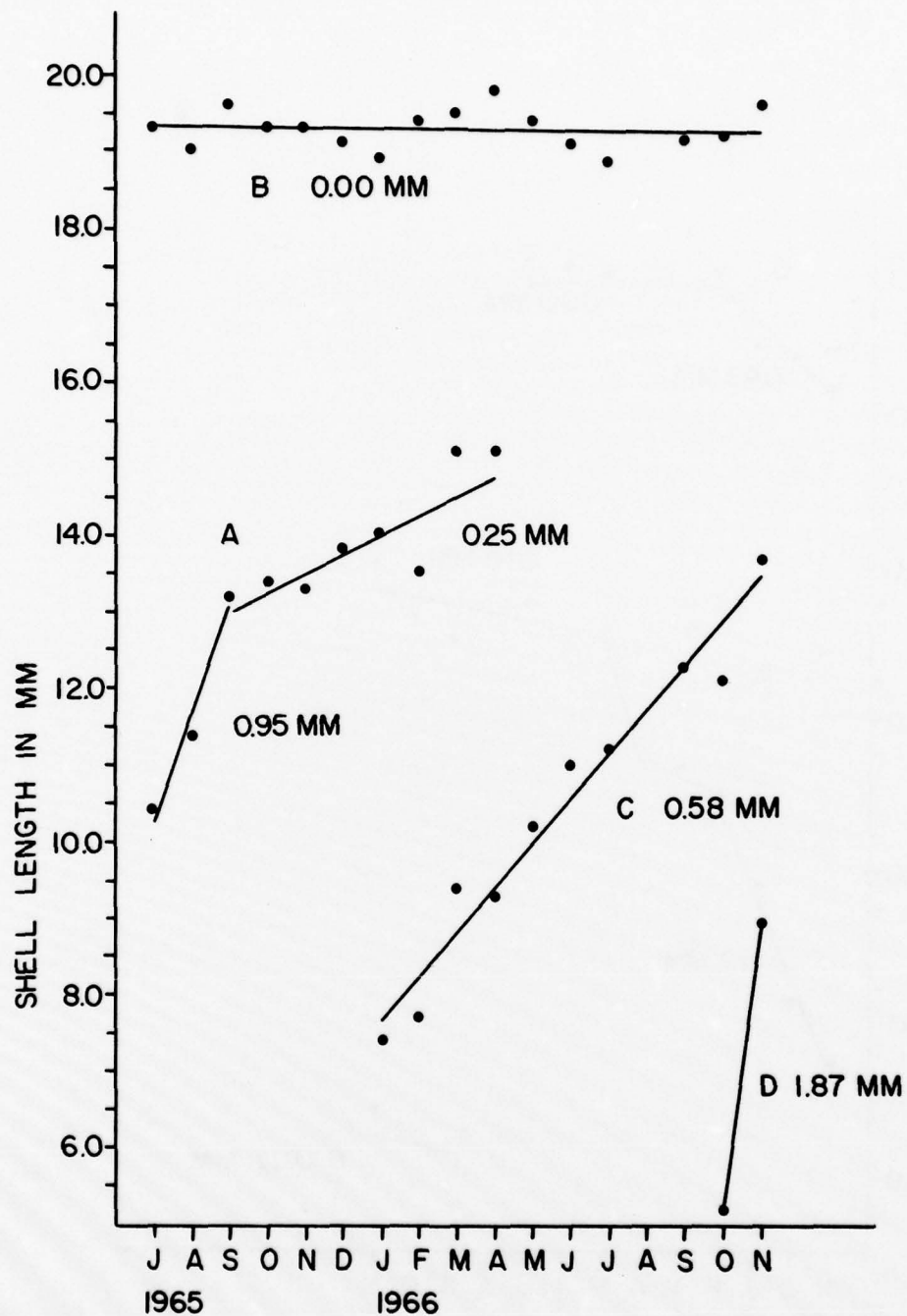


FIGURE 27 GROWTH CURVES SHOWING RATE OF GROWTH OF THE COMPONENTS PRESENT IN THE *NERITA VERSICOLOR* POPULATION AT LITTLE BAY, BARBADOS.

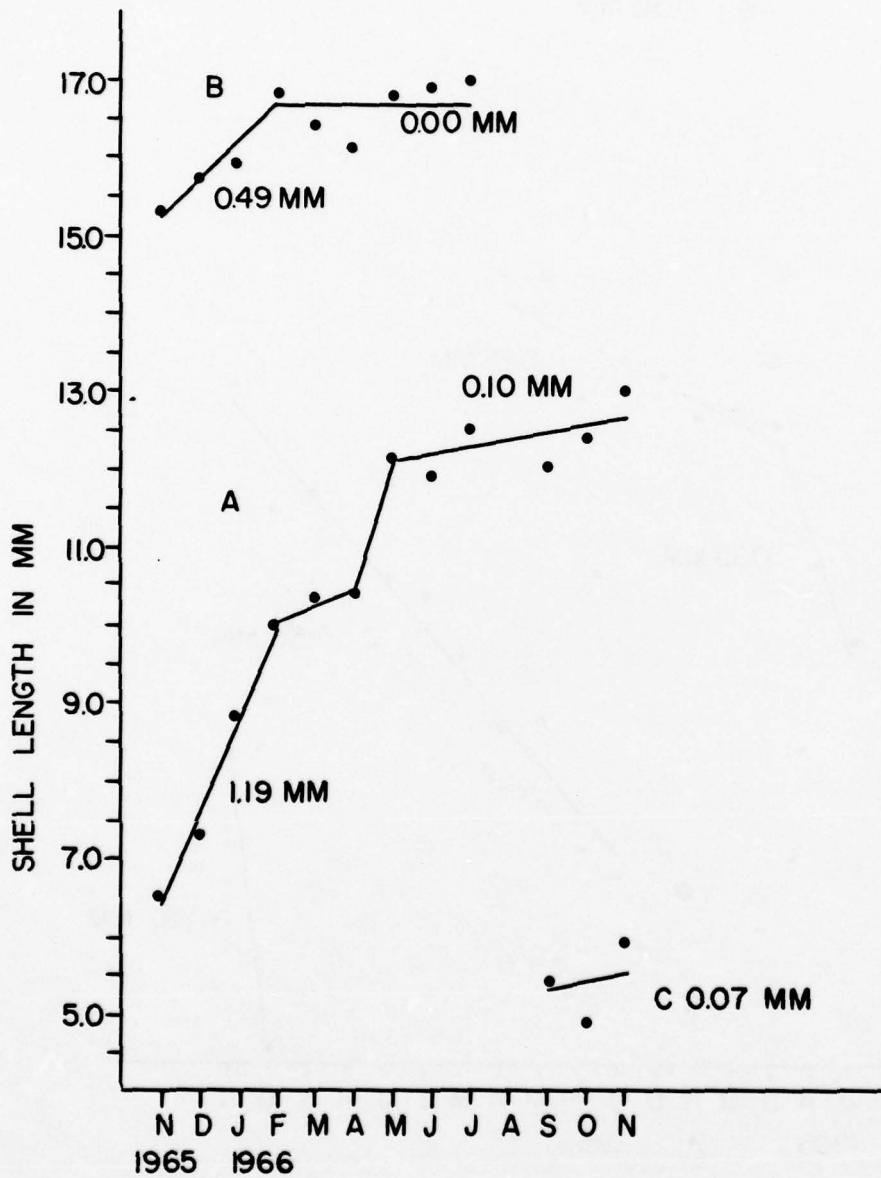


FIGURE 28 GROWTH CURVES SHOWING RATE OF GROWTH OF THE COMPONENTS PRESENT IN THE *NERITA TESSELLATA* POPULATION AT LITTLE BAY, BARBADOS.

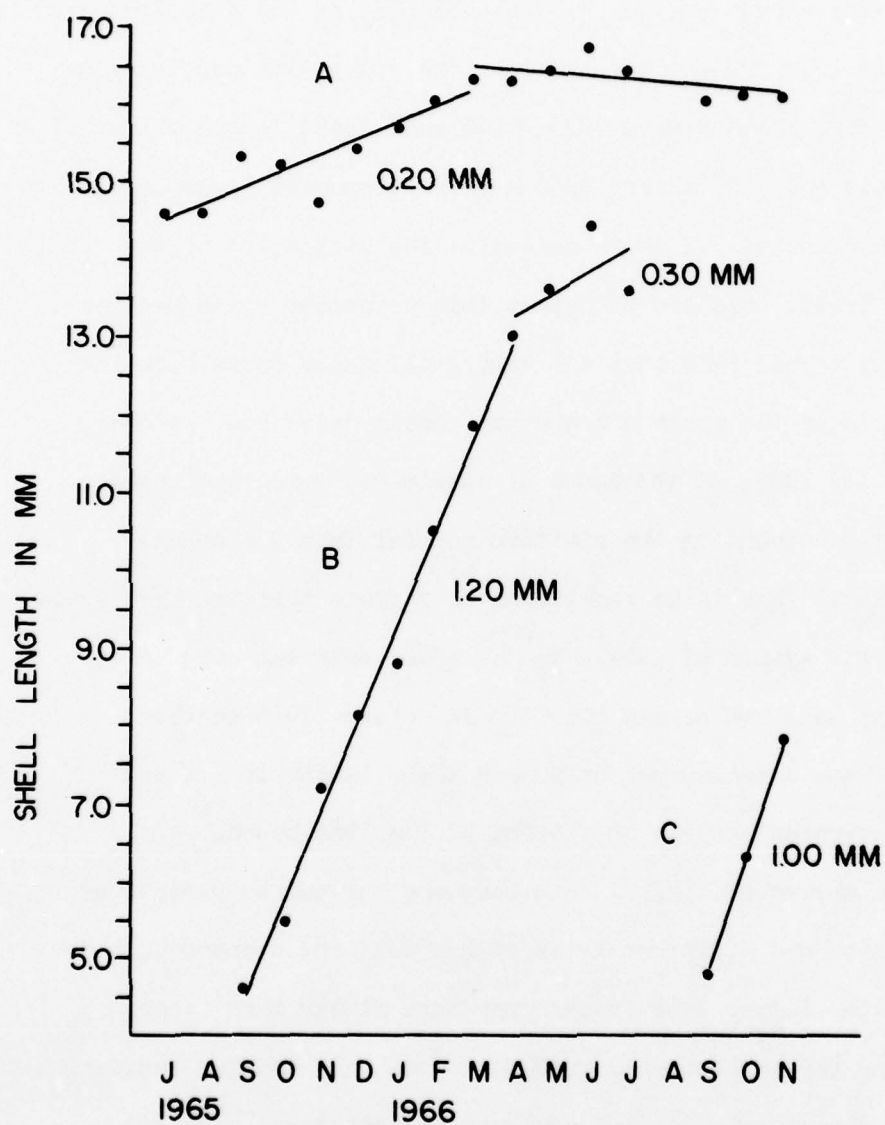


FIGURE 29 GROWTH CURVES SHOWING RATE OF GROWTH OF THE COMPONENTS PRESENT IN THE *NERITA TESSELLATA* POPULATION AT HEYWOODS BEACH, BARBADOS.

Nerita versicolor

A total of nearly 5600 animals was collected at Little Bay. The population had a definite polymodal frequency distribution. Each year class showed up as a nearly isolated mode in the size frequency distribution (Fig. 24). In July 1965, the population consisted of two components, A and B (Fig. 27), with mean shell length values of 10.4 and 19.3 mm. In January 1966 a third component C was detected with a mean value of 7.4 mm representing the settlement of the 1965 young brood. Failure to detect this component at an earlier date was due to the fact that the very small individuals hide in deep crevices of the rocks and are not easily detected. However, on November 17 1965, an abundance of specimens, measuring between 4 and 5 mm, was found on the platform not far from the actual sampling site. Thus it is reasonable to suppose that the 1966 brood settled in the autumn of 1965. In May 1966, only two components were present as A had merged with B. In October 1966 another component D was detected having a mean shell length of 5.2 mm. Component D represents the settlement of the 1966 brood.

The curves of Fig. 27 show that the various components of the population had different rates of growth. The components consisting of the larger size groups grew more slowly than those representing the smaller size groups. Hence, the younger components merge with the older which are replaced by settlement of a new brood each year. No calculated growth rate for component B was detectable. The latter population represents shells which are at least two years old and includes the largest individuals collected

(up to 23.8 mm) which must be considerably older. Growth above 19 mm proceeds only very slowly (less than .2 mm/month), as determined from tagged specimens.

The B component also included specimens which are dying off. Therefore this section of the total population is very unstable and subject to considerable variations. The growth rate of component A was .9 mm/month as the animals got larger and older. Component C grew at a rate of .6 mm/month and D at a rate of 1.9 mm/month.

There are indications that the rate of growth in N. versicolor was fairly similar in successive years; for instance, component A, possessing an initial shell length of 10.4 mm in July 1965 had a growth increment of 3.6 mm over a period of six months, and component C, having a mean value of 10.2 mm in May 1966, increased by 3.5 mm also over a period of six months.

Nerita tessellata

The frequency distributions were distinctly bimodal and the population structure was similar at the two stations (Figs. 25 and 26). A total of nearly 6300 animals was collected at Little Bay. In November 1965 the population consisted of two components, A and B, with mean values of 6.5 and 15.3 mm (Fig. 28). A and B were present in July 1966. In the sample taken in September 1966 component B was no longer present, but a new component, C, with a mean value of 5.4 was detected representing the settlement of the 1966 brood.

A total of 5500 animals was collected at Heywood's Beach. In July 1965 only one component, A, was detected with a mean value of 14.5 mm (Fig. 29). In September a new component, B, had appeared

with a mean value of 4.6 mm representing the settlement of the 1965 young brood. By September 1966 component B had merged with A and a new component, C, with a mean value of 4.8 mm was detected. Component C represents the settlement of the 1966 brood.

Certain sections of the components of the populations from the two stations are comparable as they represent the same growth period and have initially almost the same mean shell length. Component A (Fig. 28) possessing an initial shell length of 6.5 mm in November 1965, measured 12.5 mm in July 1966 and component B (Fig. 29) possessing an initial shell length of 7.2 mm in November 1965 measured 13.6 mm in July 1966. Thus there was a length increment of 5.9 mm and 6.4 mm respectively over a period of eight months. The monthly rate of growth for both components was rapid up to a shell length of 12-13 mm, then growth slowed down considerably during the summer months.

Although the growth increment over an 8-month growth period of the different components from the two localities was almost identical, the two stations showed entirely different variations in monthly growth rates. This is probably due to the difference in habitat of the two stations. The variations in growth rates were more pronounced for Little Bay.

The analysis of the random samples of N. versicolor and N. tessellata clearly indicate that distinct year classes are present. The length frequency distributions show a definite series of modes indicating the various size and age groups. It thus appears

that the random sampling method is reliable in determining the rate of growth of the younger components of the population. It is, however, an elaborate and time-consuming method which produces results that are not entirely satisfactory over the whole size range of the population.

The frequency distribution histograms for the monthly random samples from three stations in Jamaica are shown in Figs. 30 to 34.

Samples of Littorina ziczac from St. Thomas on the south coast show a unimodal distribution with very little evidence of growth increase throughout the year (Fig. 30).

The distribution of Tectarius muricatus, however, from the same station, is distinctly bimodal. Little change in the upper modal value in Tectarius was observed throughout the year (Fig. 31). Lower modal values increased from about 6 mm in February of 1966 to about 10 mm in December of the same year. This represents a monthly growth increment of about 0.4 mm. Thus two age classes appear to be present within the population of Tectarius in Jamaica. This is in contrast to single class found in Barbados where practically no young stages were observed.

The frequency distribution histograms for Nodolittorina tuberculata from Green Castle, Jamaica also appear to be bimodal (Fig. 32). Lower modal values increased from about 5 mm in February of 1966 to 8 mm in January of the following year or a monthly increment of about 0.3 mm. There was an increase in upper modal values from 7 mm in February of 1966 to about 11 mm in September of the same year or about 0.6 mm/month.

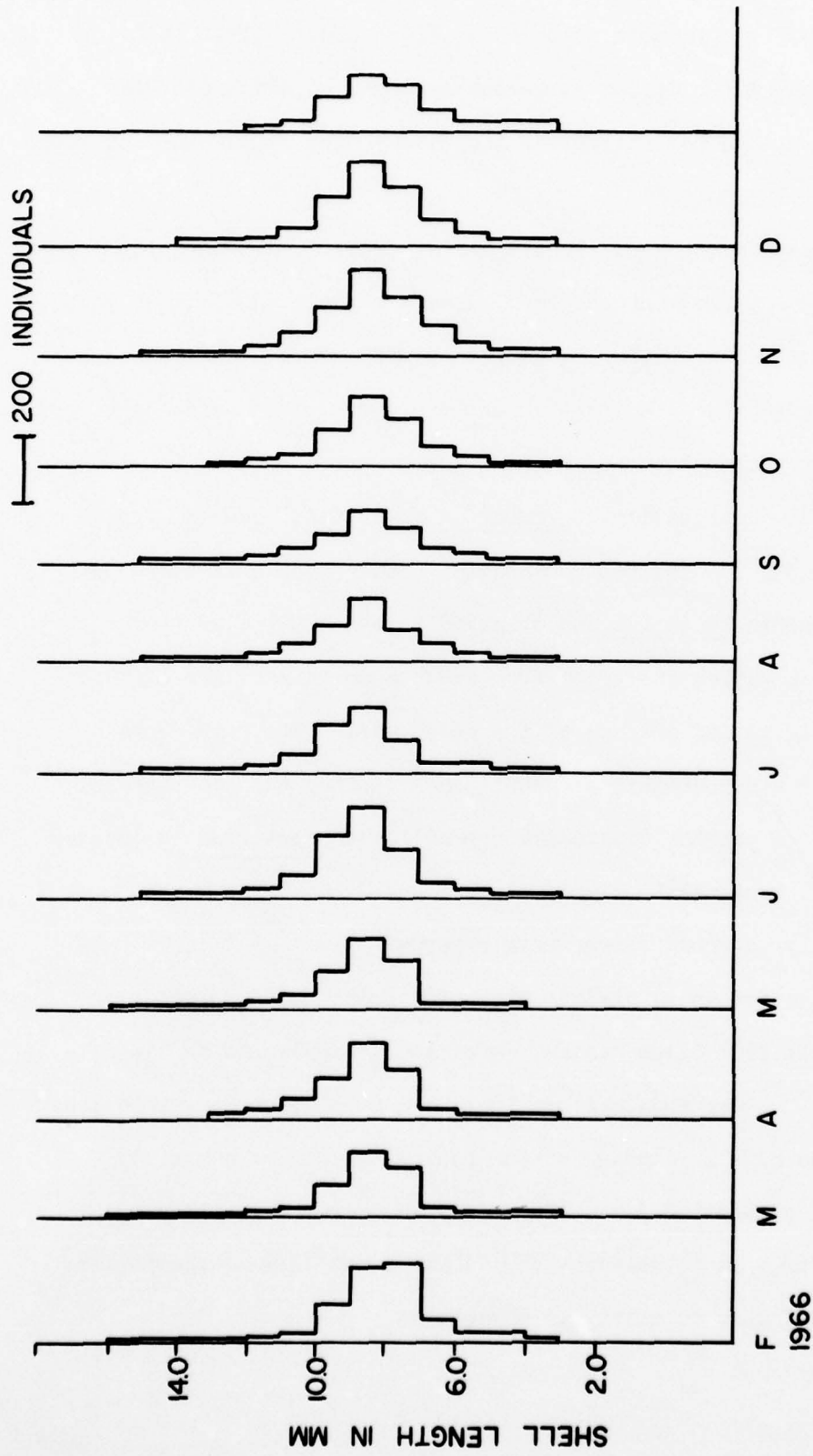
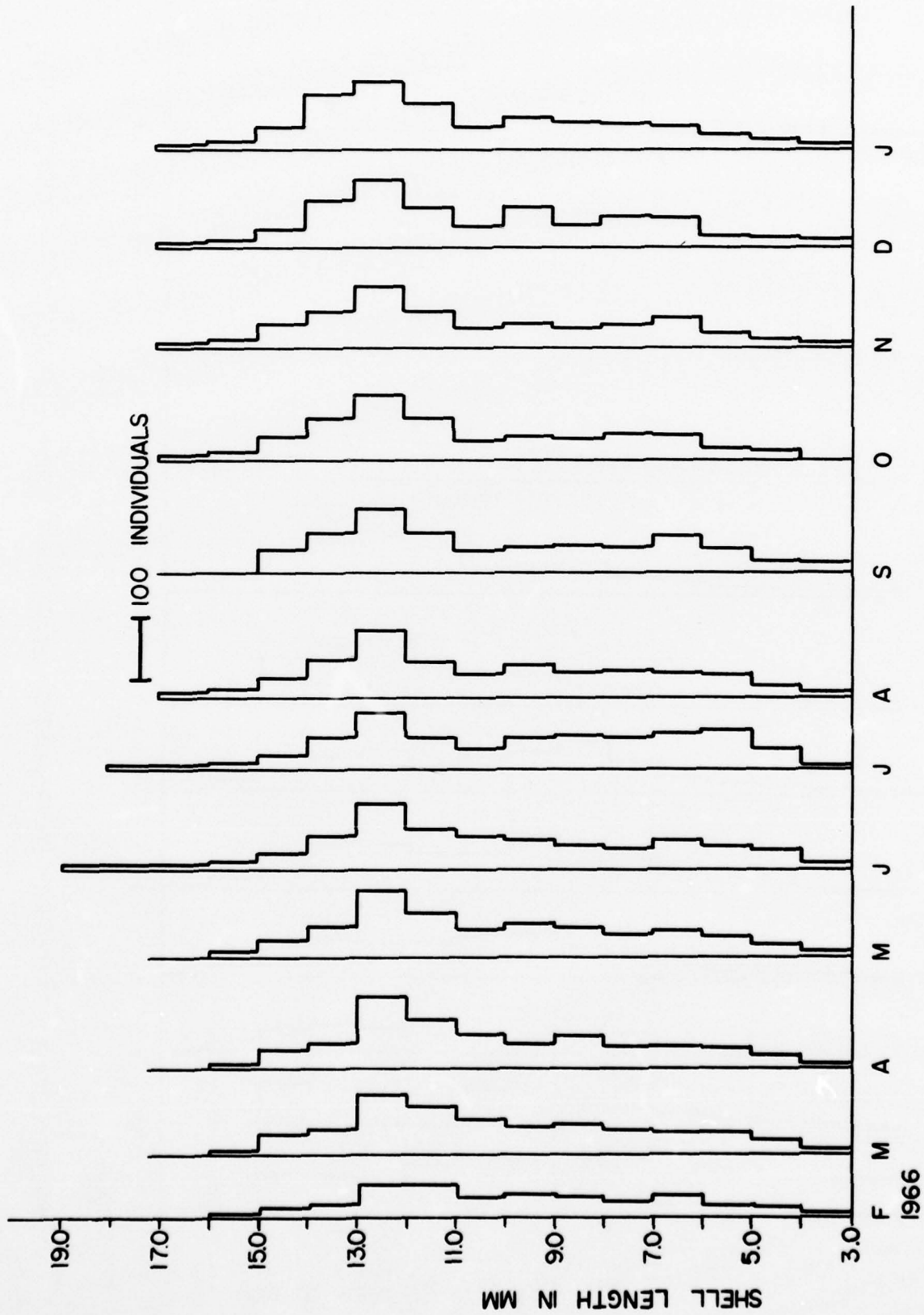
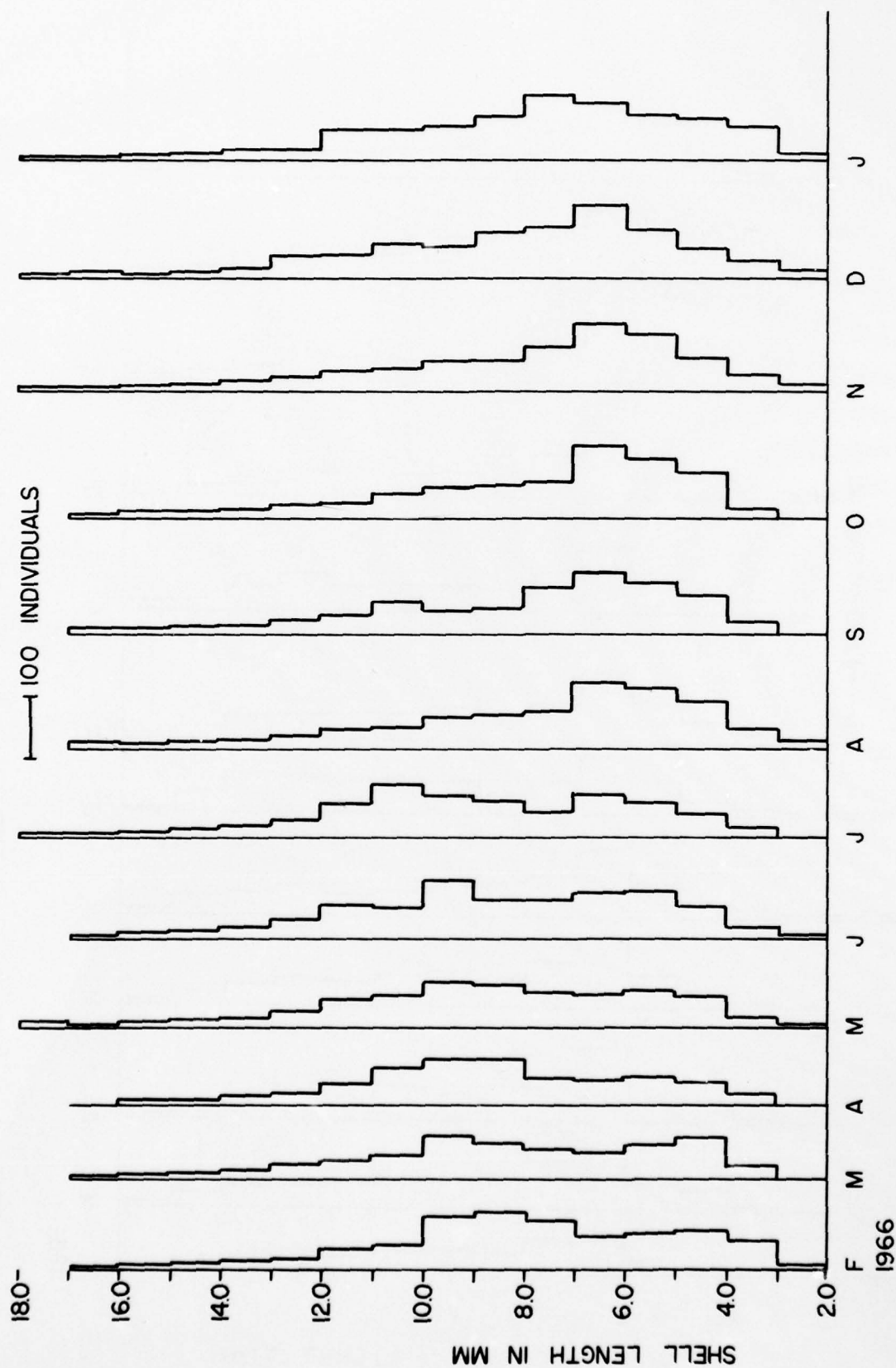


FIGURE 30 SIZE FREQUENCY DISTRIBUTIONS OF *LITTORINA ZICZAC*, ST. THOMAS, JAMAICA.

FIGURE 31 SIZE FREQUENCY DISTRIBUTIONS OF *TECTARIUS MURICATUS*, ST. THOMAS, JAMAICA.



JAMAICA
FIGURE 32 SIZE FREQUENCY DISTRIBUTIONS OF NODOLITTORINA TUBERCULATA, GREEN CASTLE.

Thus in both Nodolittorina and Tectarius the samples from Jamaica indicated slow growth throughout the year while there was no clear evidence of growth from frequency distributions in the Barbados samples of the same species.

The samples of Nerita tessellata from Morant Point, Jamaica (Fig. 33) are strongly unimodal and give very little precise information on growth throughout the year.

In Nerita versicolor, however, there is evidence that the population contains more than two age classes (Fig. 34). Because of the complexity of the size classes in this population it is difficult to determine the monthly growth increments by inspection. However, lower modal values of 4 mm in February of 1966 appear to increase to about 9 mm in January of 1967 or a monthly increment of about 0.4 mm.

B. GROWTH OF MARKED SPECIMENS

The results of the measurements of marked individuals are shown in Figs. 35-51 for Barbados and Jamaica. All regression lines are calculated from growth increments of individually marked animals according to the methods of Manzer and Taylor (1947) and Hancock (1965).

Littorina ziczac

The regression lines for yearly shell growth increase for Little Bay and Paynes Bay in Barbados and for St. Thomas in Jamaica are shown in Fig. 35. There was little difference in annual shell growth increments between Little Bay and St. Thomas. Individuals

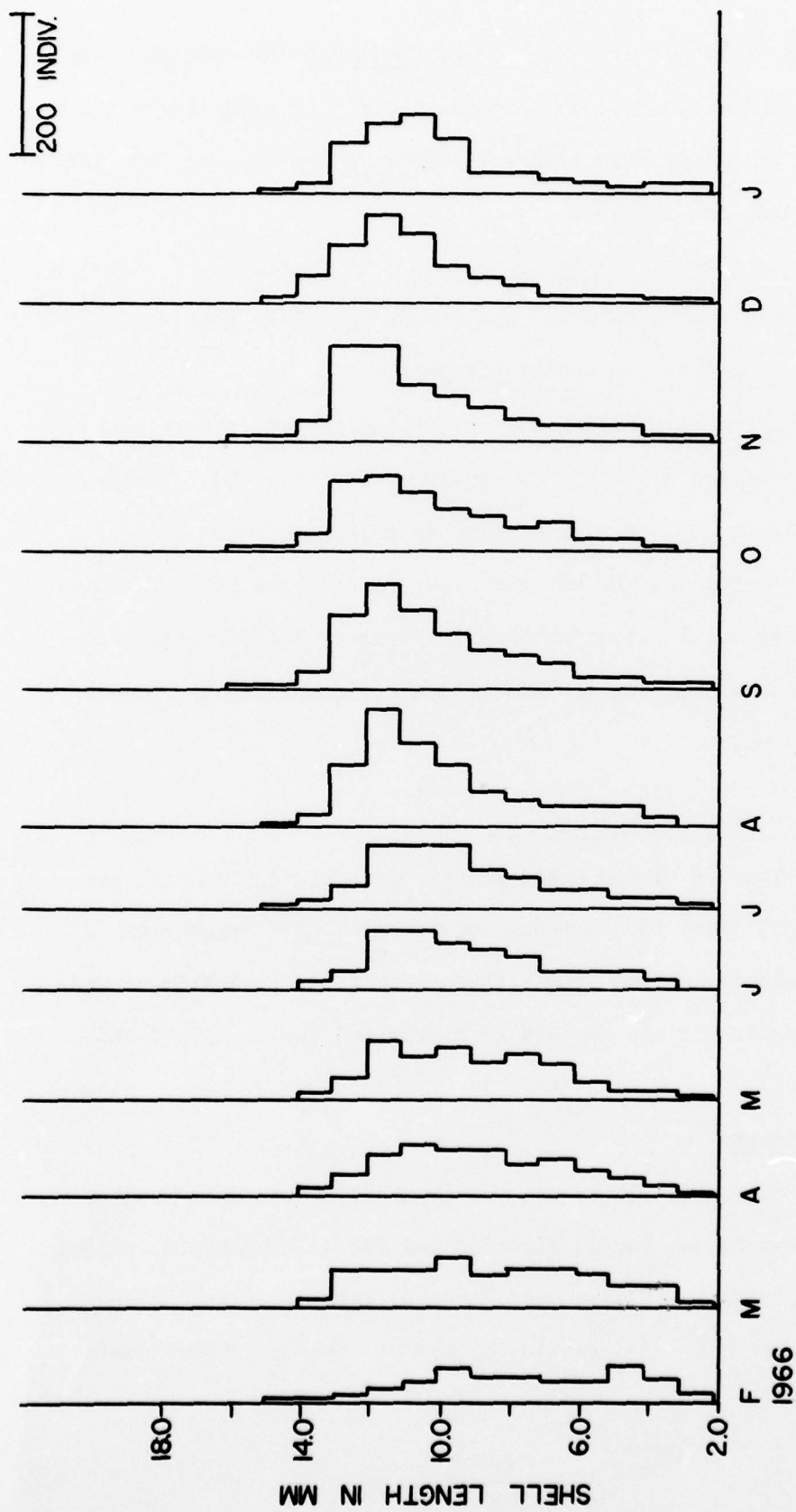


FIGURE 33 SIZE FREQUENCY DISTRIBUTIONS OF *NERITA TESSELLATA*, MORANT POINT, JAMAICA.

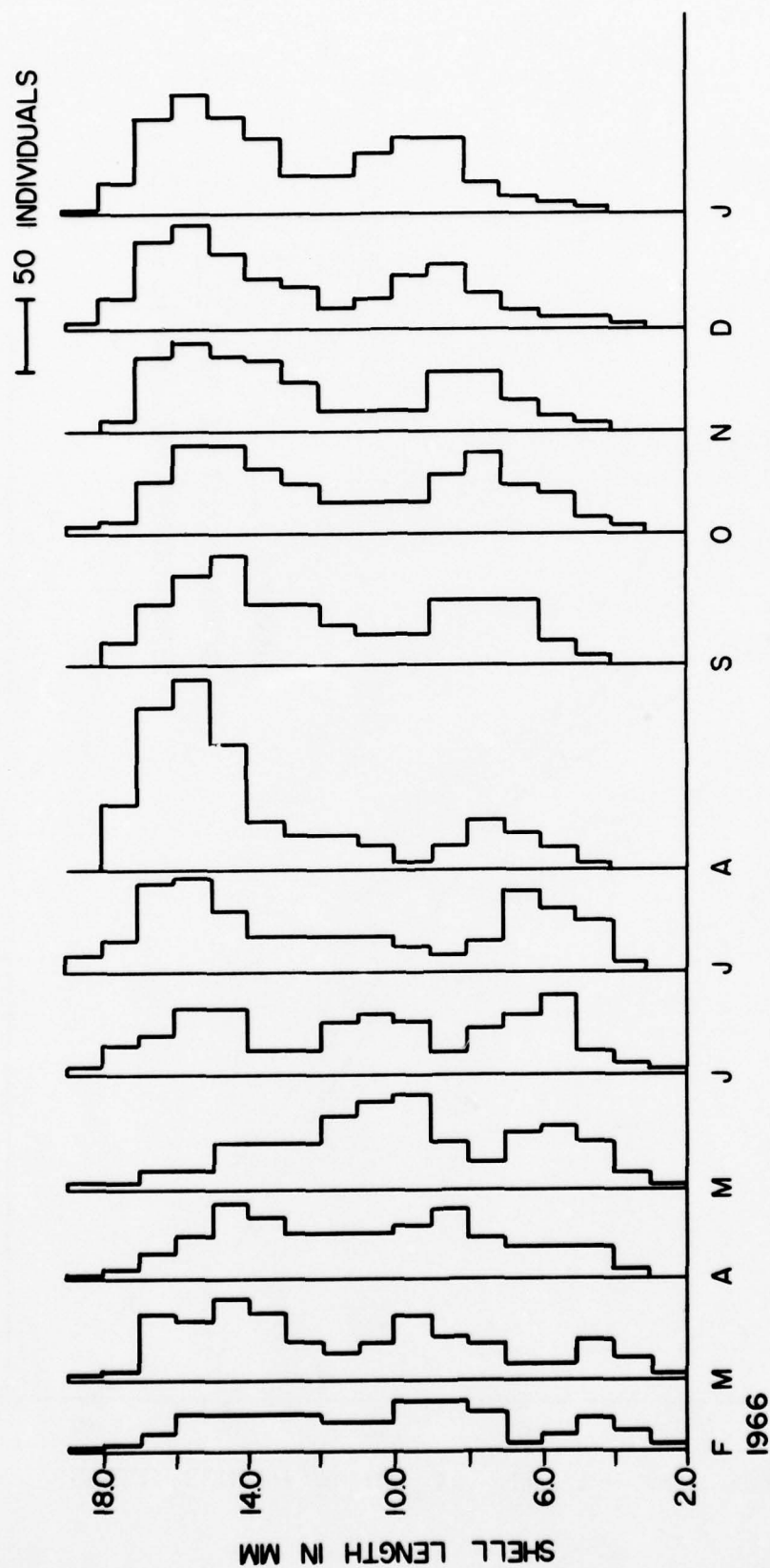


FIGURE 34 SIZE FREQUENCY DISTRIBUTIONS OF *NERITA VERSICOLOR*, MORANT POINT, JAMAICA.

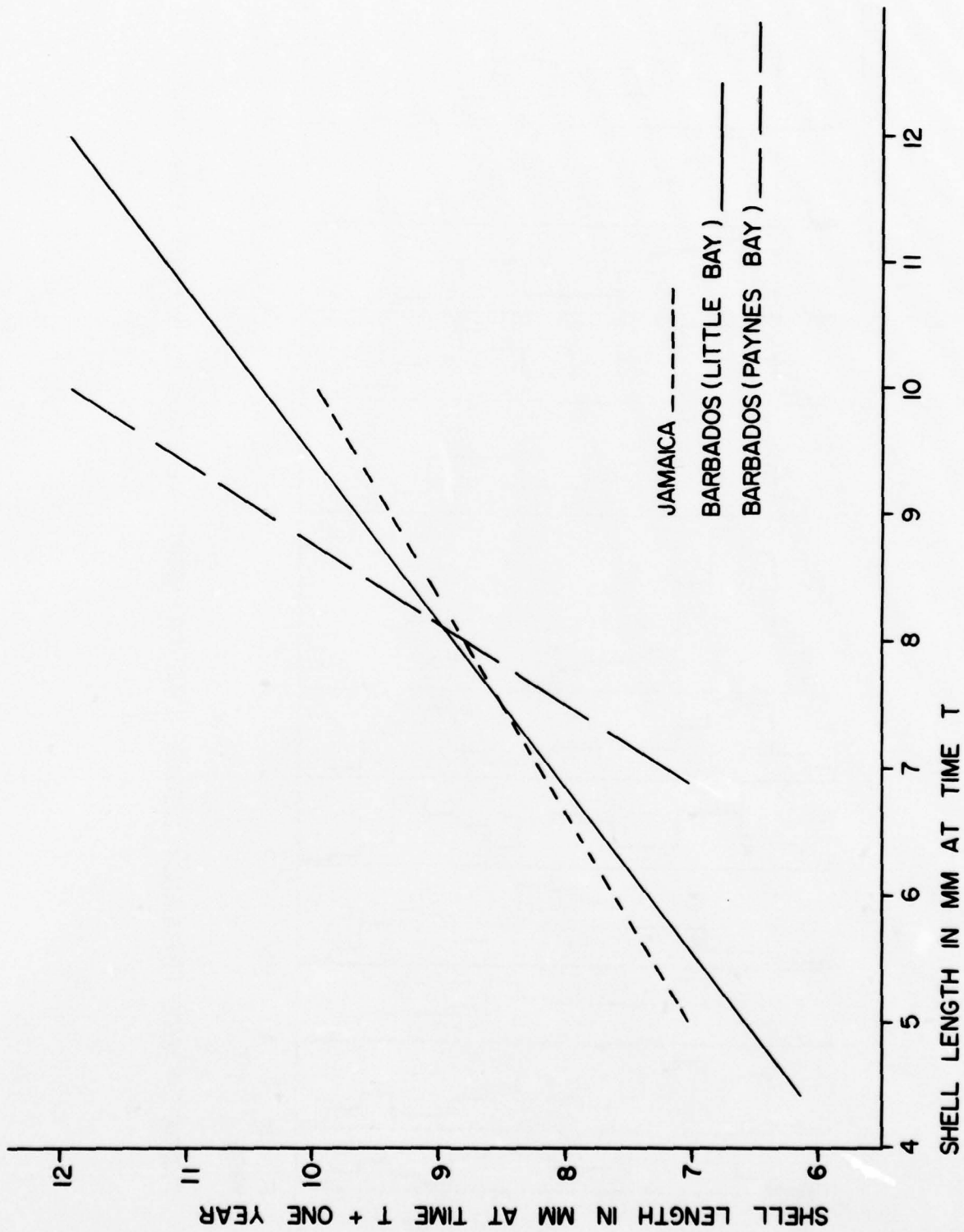


FIGURE 35 GROWTH OF LITTORINA ZICZAC.

with an initial shell length of 5 mm reached a size of 7 mm in one year in Jamaica, while at Little Bay they attained a size of 6.6 mm. A notable difference in growth rates was found in the population from Paynes Bay, Barbados however. Individuals with an initial measured shell length of 7 mm were only 7.2 mm long at the end of a year, while those with an initial shell length of 10 mm grew a full 2 mm at Paynes Bay in one year and reached a larger size than the group from Little Bay. The regression coefficients of the two lines were significantly different at the level P.01. Relevant equations for regression lines were as follows:-

Little Bay	-	$y = 2.8192 + 0.7641x$
Paynes Bay	-	$y = 4.13 + 1.62x$
St. Thomas	-	$y = 3.56 + 0.5321x$

Nodolittorina tuberculata

The regression lines for shell length growth over a period of one year for Nodolittorina from Little Bay in Barbados and from St. Thomas in Jamaica are shown in Fig. 36. There was little difference between St. Thomas and Little Bay in shell growth. Individuals with initial shell lengths of 5 mm increased in shell length to 6.2 mm in Barbados and 6.5 mm in Jamaica in one year. Individuals with initial shell lengths of 11 mm increased to 11.5 and 11.6 mm in one year in Barbados and Jamaica respectively. The relevant equations for the regression lines are as follows:-

Barbados	-	$y = 1.72 + 0.8841x$
Jamaica	-	$y = 2.53 + 0.8230x$

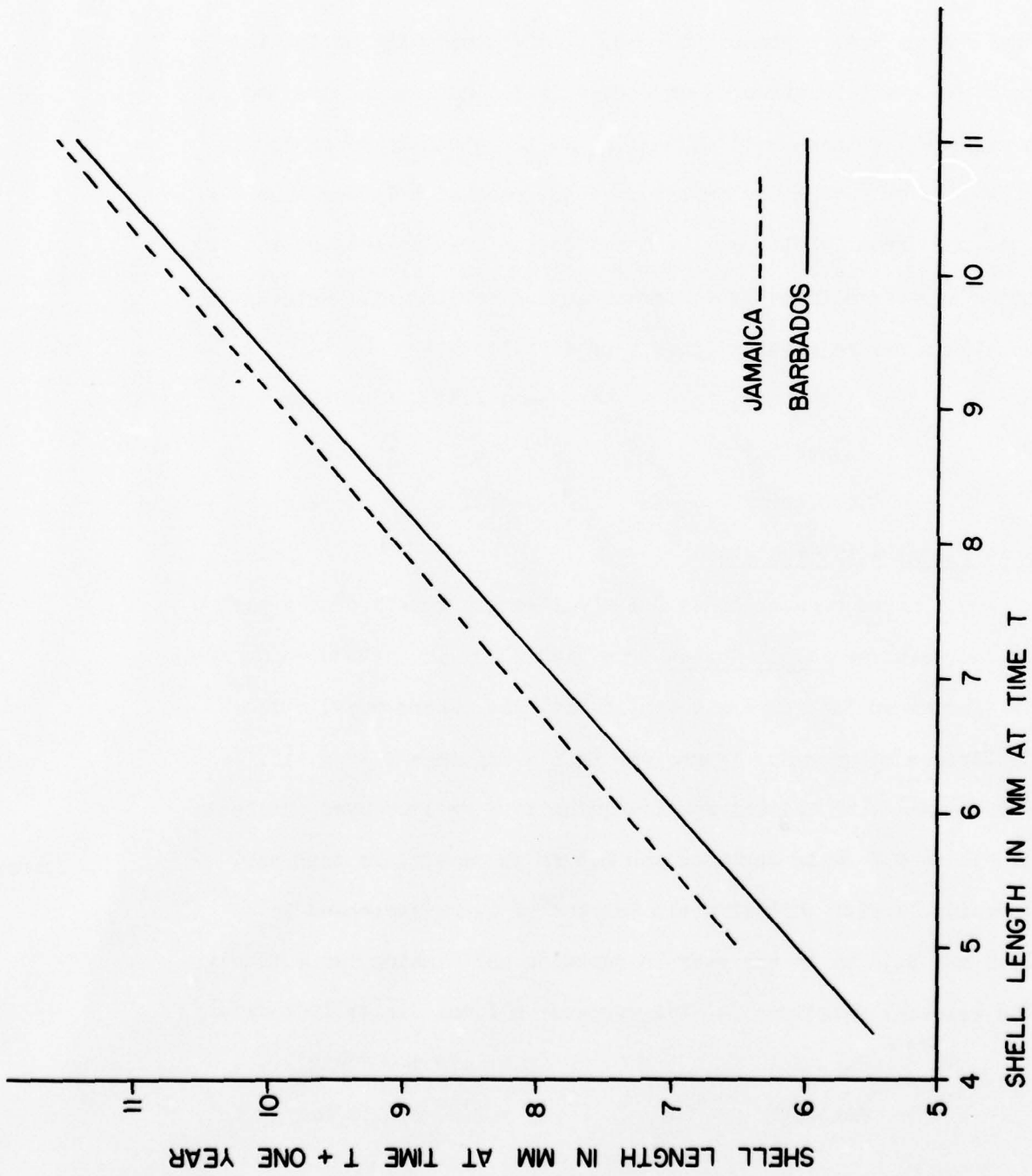


FIGURE 36 GROWTH OF NODOLITTORINA TUBERCULATA.

Tectarius muricatus

Regression lines for shell length growth in one year for Tectarius in Barbados are shown in Fig. 37. Growth of Tectarius in Barbados was found to be very slow in individuals larger than 10 mm. It should be noted that juveniles of this species were seldom found at any of the stations in Barbados. A steady increase of only 0.4 mm/year from sizes 15 mm to 24 mm was observed.

A sample of Jamaica specimens which were transplanted to Barbados showed, however, high growth rates (Fig. 37) when compared with the growth of the Barbados native forms. Individuals with an initial shell length of 10 mm reached a size of nearly 17 mm in one year while large specimens of initial shell length of 21 mm attained a size of 23.6 mm in one year. The fact that transplanted specimens grew faster than the local Barbadian population indicates that the environment is not in itself limiting to growth. A possible alternative explanation for the very slow growth of Tectarius in Barbados is that the local population is one which has existed for a long period and the individuals themselves are very old. The fact that few juvenile stages of this species were found in Barbados suggests that little recruitment is taking place in the population. The stable form of the size frequency distribution histograms of Fig. 23 also supports the hypothesis of an old, slow-growing population.

The growth of Tectarius in Jamaica is shown in Fig. 38. The sizes of individuals tagged were smaller than those studied in Barbados and the regression lines for both 1966 and 1967 indicate

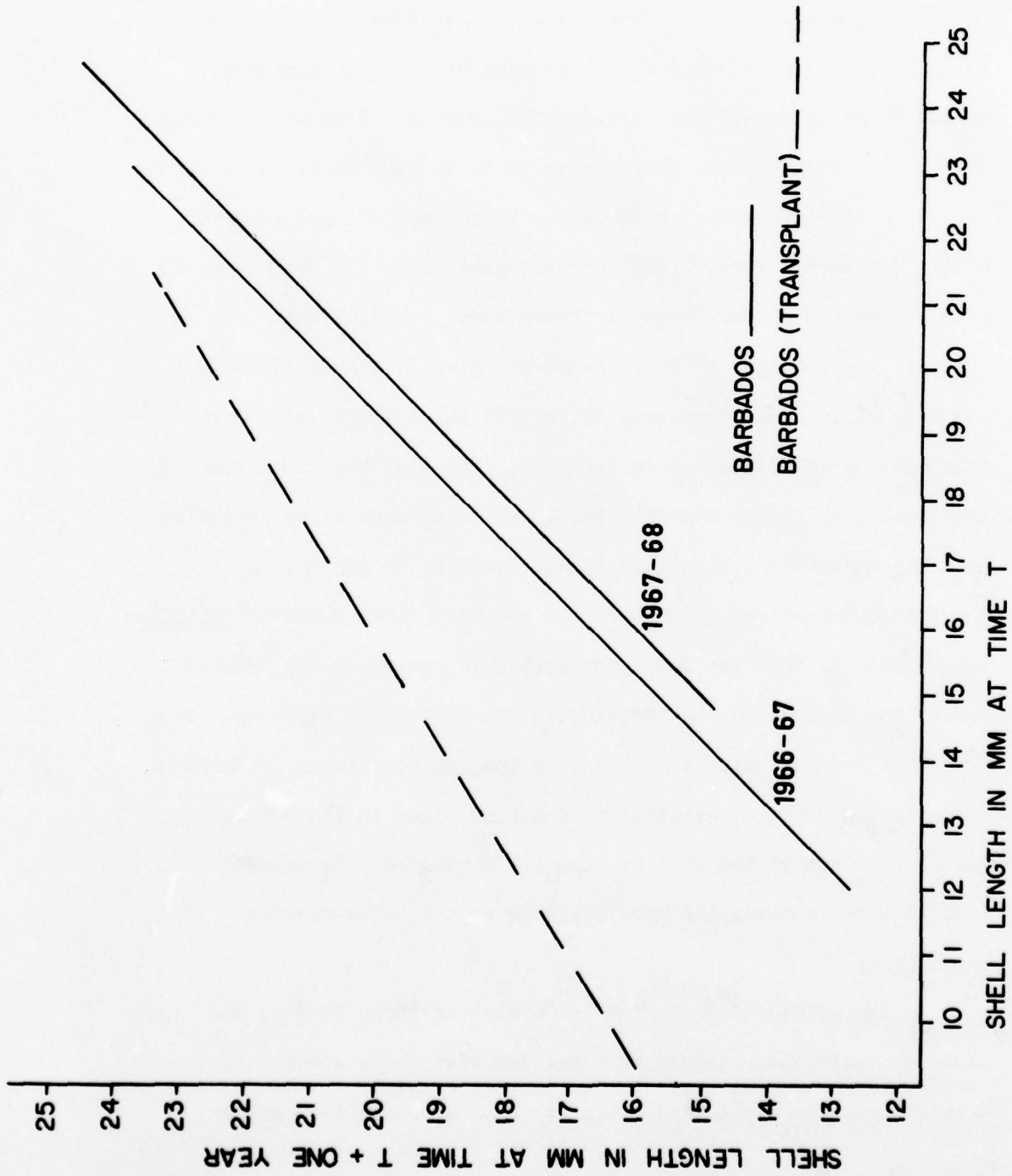


FIGURE 37 GROWTH OF TECTARIUS MURICATUS, BARBADOS.

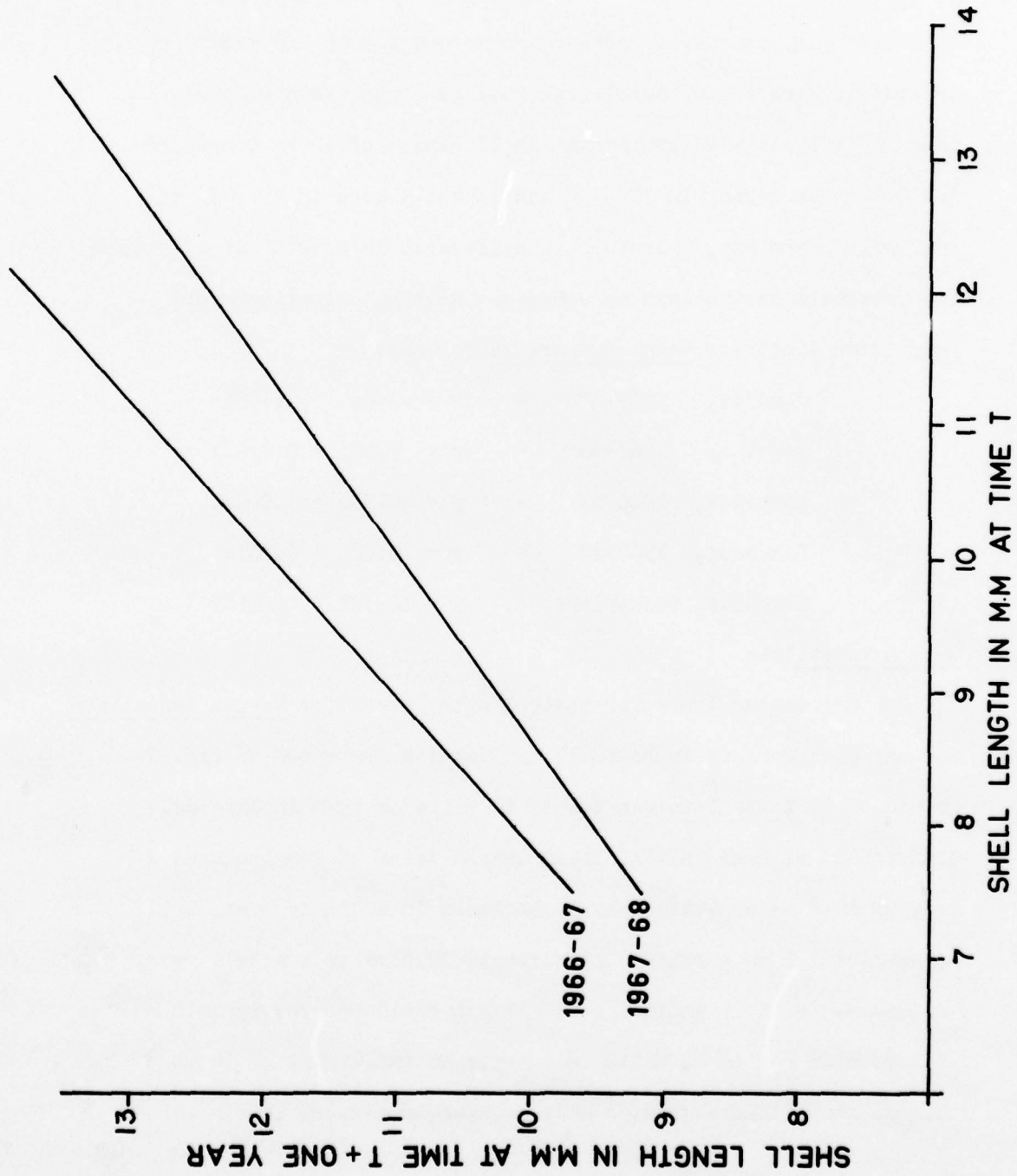


FIGURE 38 GROWTH OF TECTARIUS MURICATUS, JAMAICA

rather rapid growth rates in the smaller sizes. Thus individuals with an initial size of 8 mm reached a shell length of 9.5 and 10.2 mm in a single year in 1966 and 1967 respectively. Individuals of slightly larger size, however, grew more slowly and growth increments were approximately the same as in Barbados samples. Thus individuals with an initial shell length of 12 mm increased to 12.4 mm in a year in 1967-68 and slightly more in 1966-67 to 13.7 mm. There was, therefore, a difference in growth rates between the two years in the Jamaica samples. Relevant equations for regression lines for Tectarius are as follows:

Jamaica, 1966-67	-	$y = 2.86 + 0.9056x$
Jamaica, 1967-68	-	$y = 3.84 + 0.7157x$
Barbados, 1966-67	-	$y = 0.754 + 0.0048x$
Barbados, 1967-68	-	$y = 0.02 + 1.001x$
Barbados, transplant	-	$y = 10.334 + 0.6158x$

Nerita tessellata

Regression lines for shell length growth for Nerita tessellata for one year periods in Barbados and Jamaica are shown in Fig. 39. Growth of N. tessellata was faster in Barbados than in Jamaica. Individuals with an initial shell length value of 9 mm reached a size of 14.2 mm at Little Bay in Barbados in a single year, while in Jamaica a 9 mm specimen only grew to 12.6 mm in a single year. Individuals with an initial shell length of 15 mm grew to 16.5 mm in a year in Barbados, while in Jamaica an individual of 14 mm initial shell length grew to only 14.2 mm in a year.

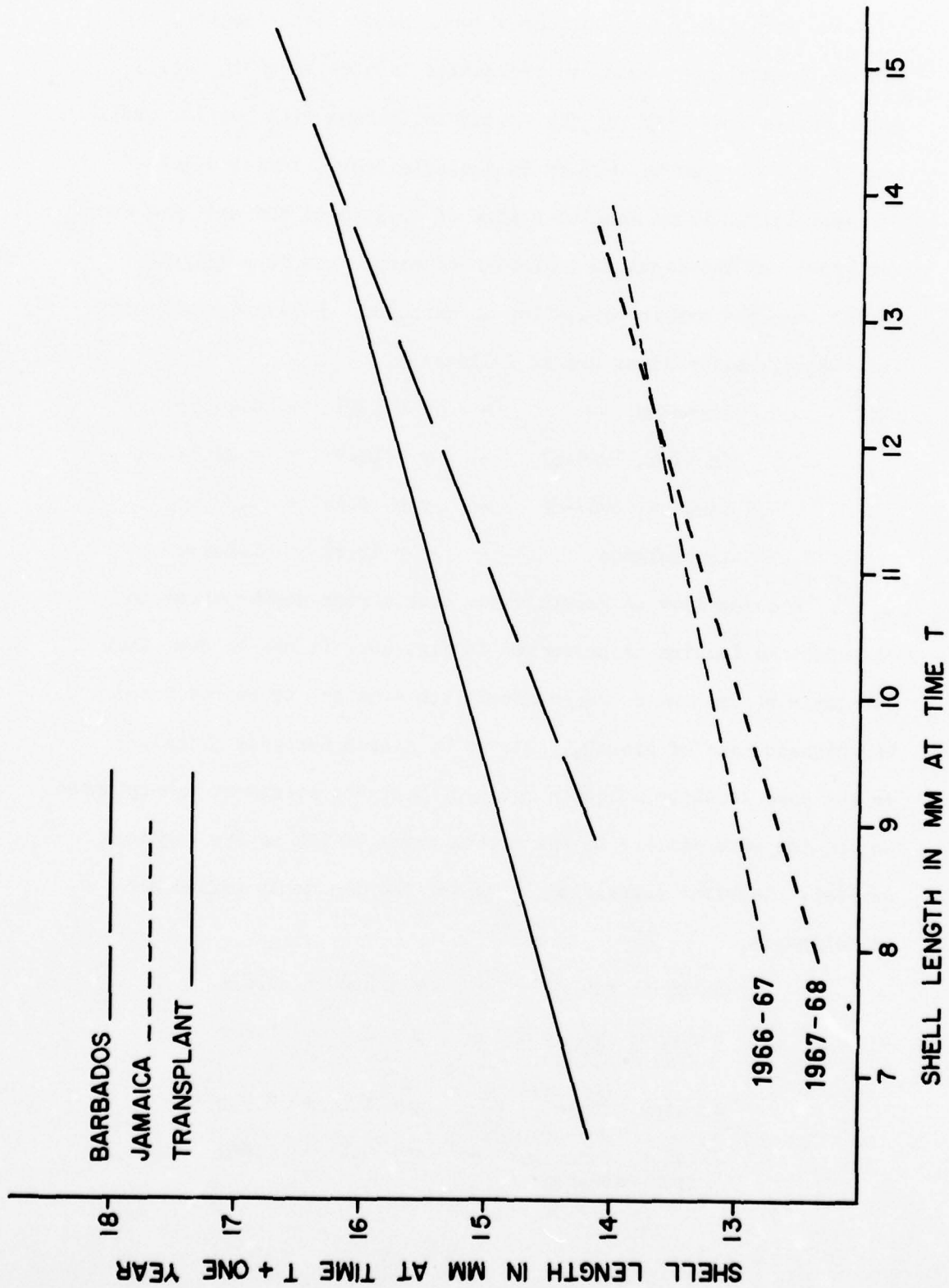


FIGURE 39 GROWTH OF NERITA TESSELLATA.

A population sample of N. tessellata was transplanted to Barbados from Jamaica. The regression line of shell length growth for the transplanted Jamaican population is also shown in Fig. 39. Young stages grew very rapidly and an individual with initial shell length of 7 mm grew to 14.3 mm in a single year. Individuals of shell length 14 mm reached a size of 16.3 mm at the end of a year. The growth of the Jamaican transplanted sample was thus slightly faster than the native population in Barbados. Relevant equations for the regression lines are as follows:-

Barbados	-	$y = 10.5 + 0.4065x$
Jamaica, 1966-67	-	$y = 10.97 + 0.2213x$
Jamaica, 1967-68	-	$y = 9.94 + 0.3058x$
Transplants	-	$y = 12.28 + 0.2864x$

A comparison of growth rates over a four month period in Barbados and Jamaica is presented in Fig. 40. It may be seen that a sample of specimens transplanted from Jamaica to Barbados had the highest rate of growth, followed by native Barbados animals in the same locality. Growth rates of Barbados specimens transplanted to Jamaica were similar to the growth rates of the native Jamaican samples. Relevant regression lines for the four month period are as follows:-

Barbados native	-	$y = 3.4 + 0.87x$
Barbados transplant from Jamaica	-	$y = 0.5 + 1.25x$
Jamaica native	-	$y = 1.6 + 0.93x$
Jamaica transplant from Barbados	-	$y = 0.4 + 1.06x$

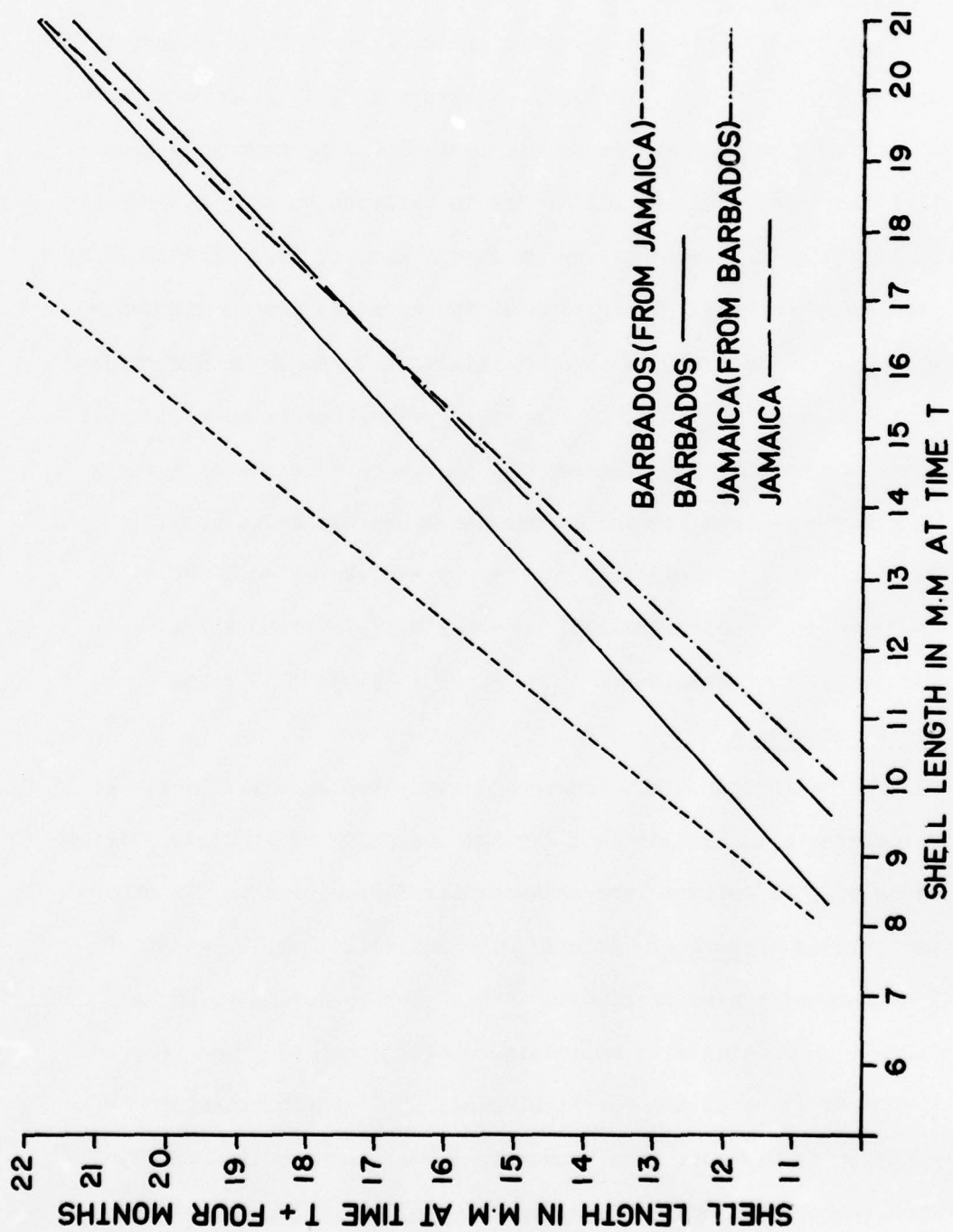


FIGURE 40 GROWTH OF NERITA TESSELLATA.

Nerita versicolor

Regression lines showing growth rates of shell length of N. versicolor from Barbados and Jamaica are shown in Fig. 41. The two regression lines for Barbados indicate growth over a period of one year each in 1966 and 1967. Growth was similar in both years. Individuals with an initial shell length of 9 mm reached a size of 17 mm in one year at Little Bay in Barbados, while individuals of initial shell length 21 mm reached a size of 21.2 to 22.2 mm at the end of a year. The growth of the Jamaican sample was somewhat lower. Specimens with an initial shell length of 9mm reached a size of 14 mm at the end of a year, while those with an initial shell length of 15 mm reached only 18.2 mm at the end of a year. Relevant equations for the regression lines are as follows:-

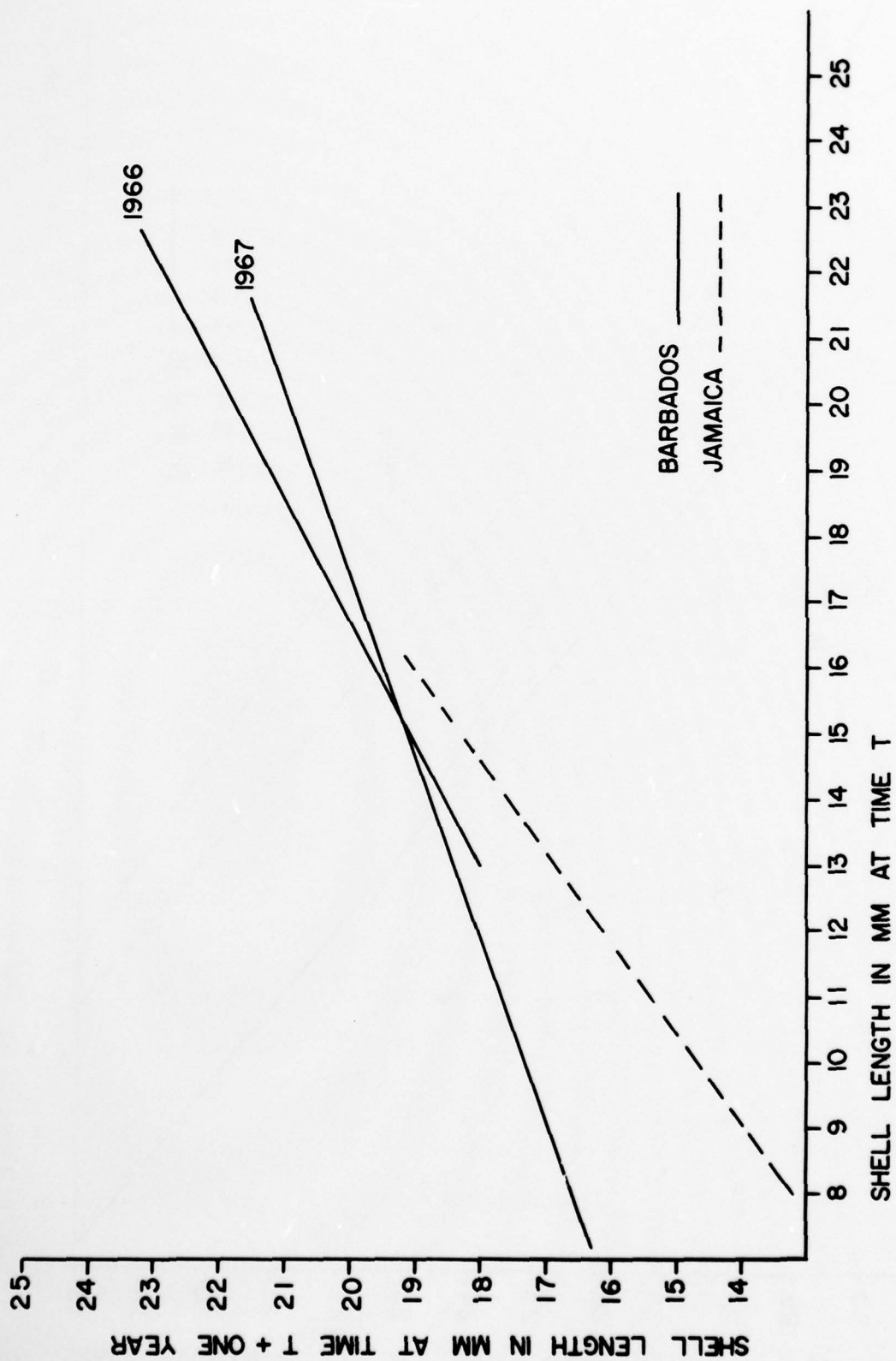
$$\text{Barbados 1966} \quad - \quad y = 11.24 + 0.5269x$$

$$\text{Barbados 1967} \quad - \quad y = 13.74 + 0.3579x$$

$$\text{Jamaica} \quad - \quad y = 7.03 + 0.7625x$$

Nerita peloronta

Regression lines showing growth rates of shell length of N. peloronta in Barbados and Jamaica are shown in Fig. 42. Growth rates of this species were considerably faster than in the other two species of Nerita. Animals with an initial shell length of 9 mm reached a size of 18.5 mm in one year in Barbados, while animals in Jamaica with an initial shell length of 12 mm reached a size of 18 mm during the first year. The growth rates of Jamaican populations were, however, slower in both 1966 and 1967 than the populations in Barbados. Among the larger individuals

FIGURE 41 GROWTH OF *NERITA VERSICOLOR*.

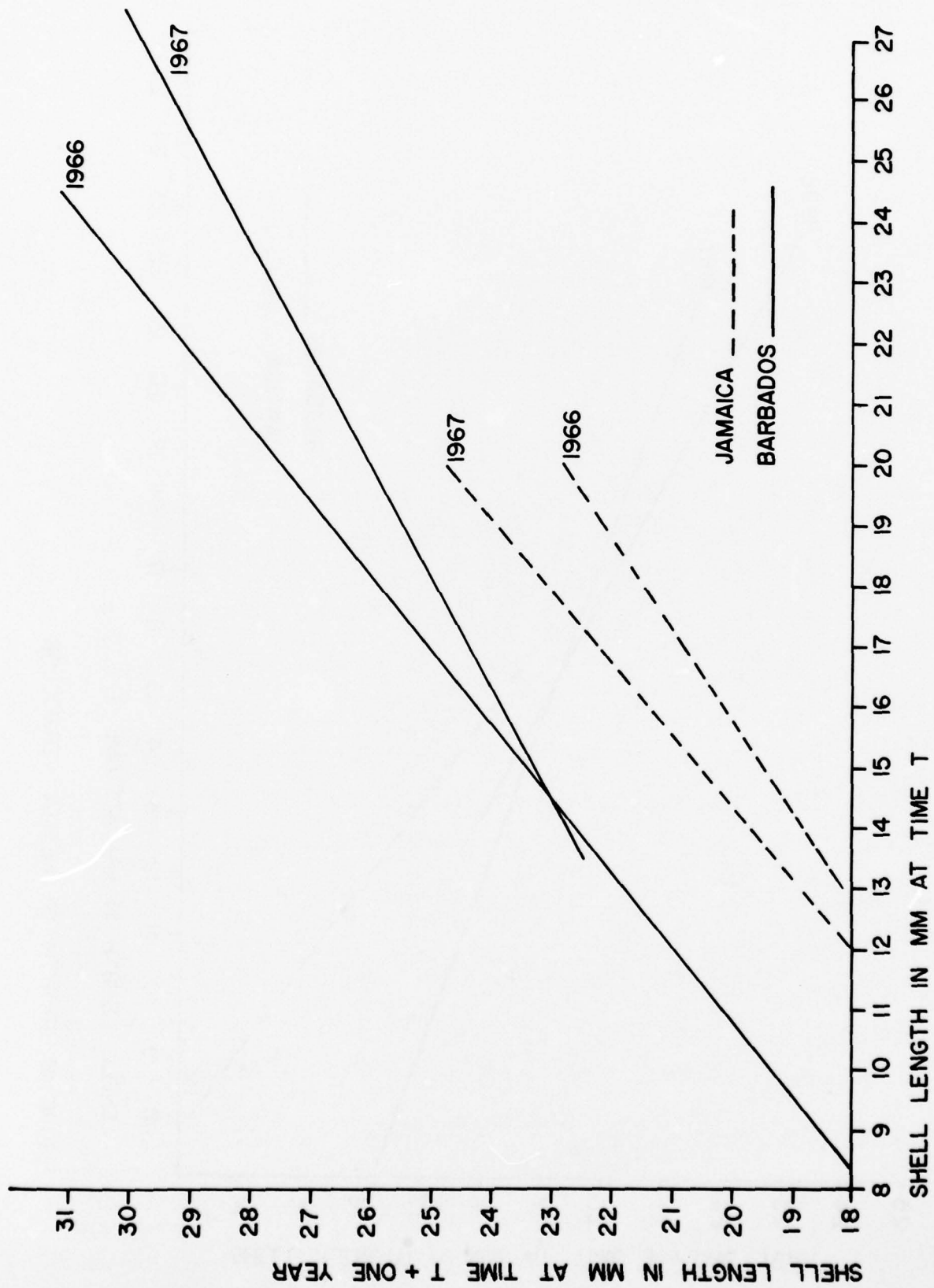


FIGURE 4.2 GROWTH OF NERITA PELORONTA.

in both areas, specimens of 20 mm initial length attained sizes of 22.8 mm in 1966 in Jamaica and 24.8 in 1967. In Barbados growth was slower in the large shell length ranges in 1967 than in 1966. Specimens with an initial shell length of 24 mm reached a size of 30.8 mm (1966) and 28.2 mm (1967) in a single year. Relevant equations for the regression lines are as follows:-

$$\text{Barbados 1966} \quad - \quad y = 11.42 + 0.8021x$$

$$\text{Barbados 1967} \quad - \quad y = 15.11 + 0.5463x$$

$$\text{Jamaica 1966} \quad - \quad y = 9.58 + 0.6651x$$

$$\text{Jamaica 1967} \quad - \quad y = 7.68 + 0.8541x$$

C. SEASONAL VARIATIONS IN GROWTH

Seasonal differences in growth rates in the genus Nerita have been reported from Miami by Kolipinski (1964) who found that growth was slowest during the months of December and January and fastest in the late summer. He considered that growth rates were directly related to seasonal temperature changes and possibly to reproductive activity. He showed that mean monthly sea and air temperatures were nearly 10°C higher in summer than in winter. However, his results are founded only upon a single, arbitrarily chosen shell size for each species and may not be true for all size ranges.

Axelsen (1968) also considered that there were small seasonal differences in growth rates of three species of Nerita in Barbados. However, his conclusions were also based on a few size ranges. Furthermore, the results were determined on a small

sample and the statistical significance of his differences was not established. Chislett (1969) found no such seasonal difference from two localities in Barbados.

By using the Manzer and Taylor plots (1947) for computing regression lines at intervals of one month instead of one year it is possible to show monthly growth rates for all sizes of individuals throughout the year. Because growth rates were so slow in the species Littorina ziczac, Nodolittorina tuberculata and Tectarius tuberculata the monthly growth increments were exceedingly small. It was therefore not possible to analyse their monthly growth rates by plotting monthly increments. The regression lines of monthly growth increments for three species of Nerita in Barbados are shown in Figs. 43 to 45. No statistically significant differences in regression coefficients at the P.05 level between any pairs of lines within families could be detected. It is, therefore, apparent that there was not any seasonal variation in growth rates in these samples of either Nerita tessellata, N. versicolor or N. peloronta in Barbados.

Similar regression lines for monthly growth intervals for all three species of Nerita in Jamaica are shown in Figs. 46 to 48. No statistically significant differences in regression coefficients at the P.05 level between pairs of lines were detected for Nerita peloronta or N. versicolor. In N. tessellata, however, regression lines for the months of May and June were significantly different from each of the rest of the family of lines at the level P.05. Growth of N. tessellata in May and June was, therefore, slightly

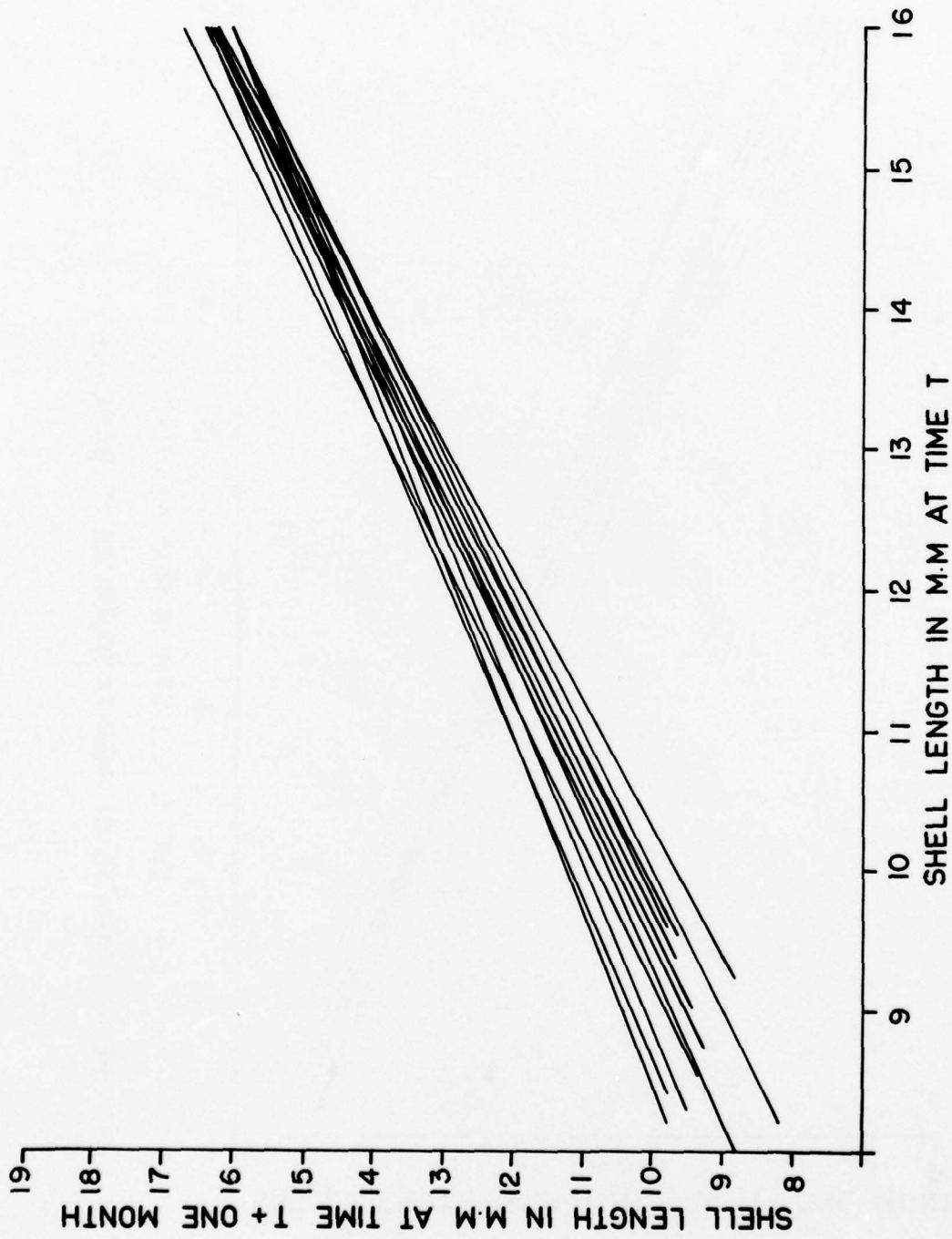
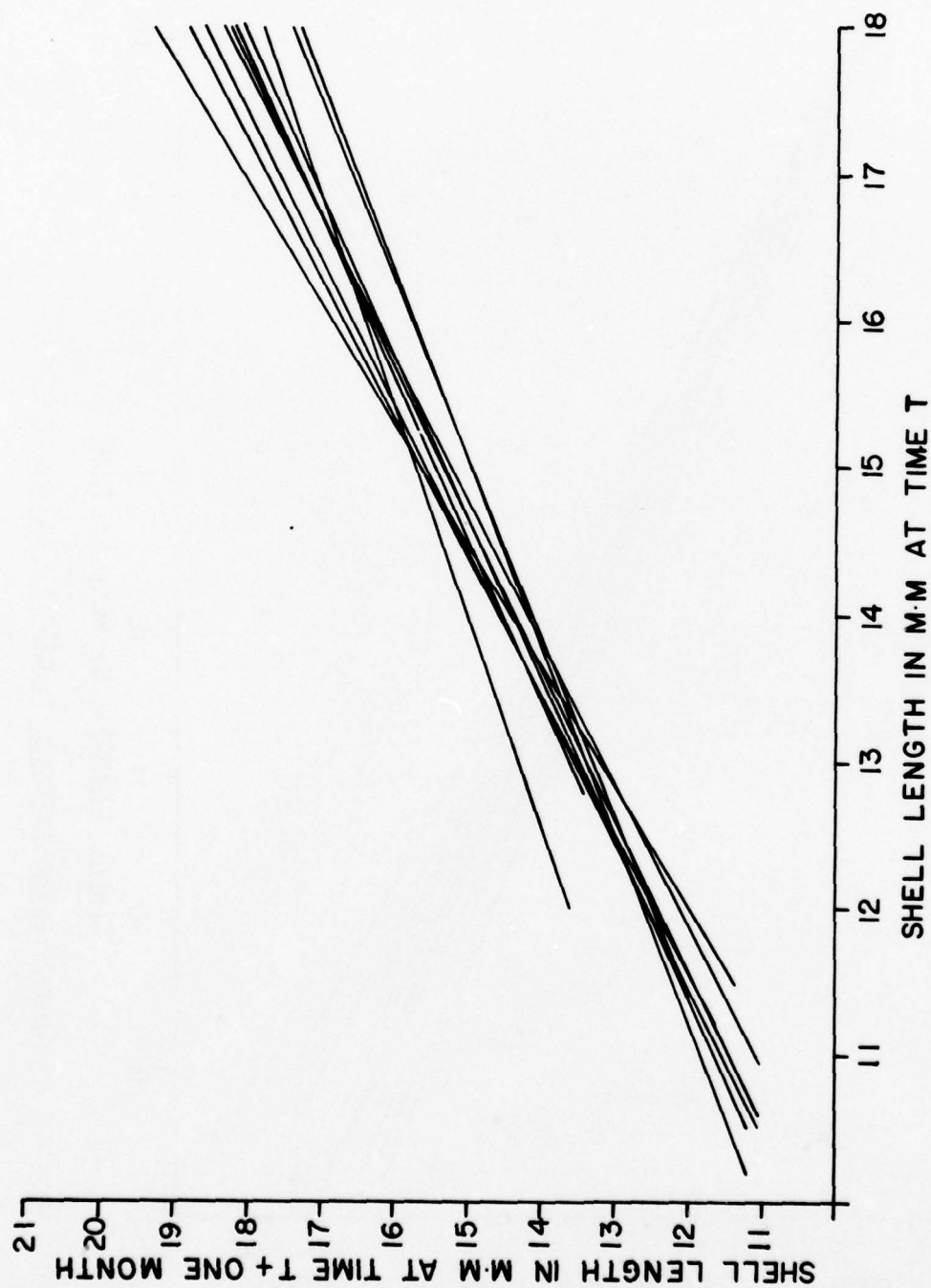
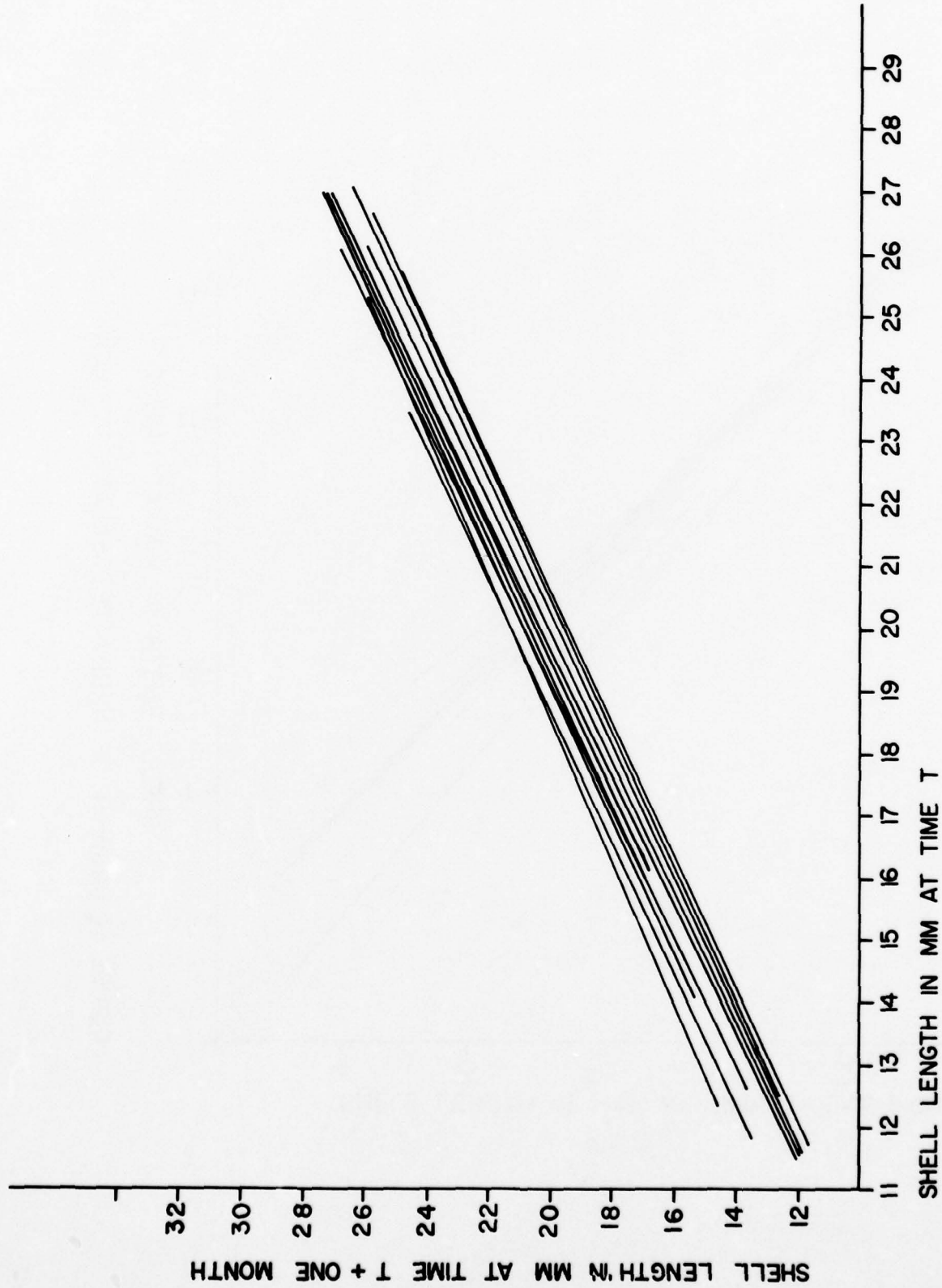
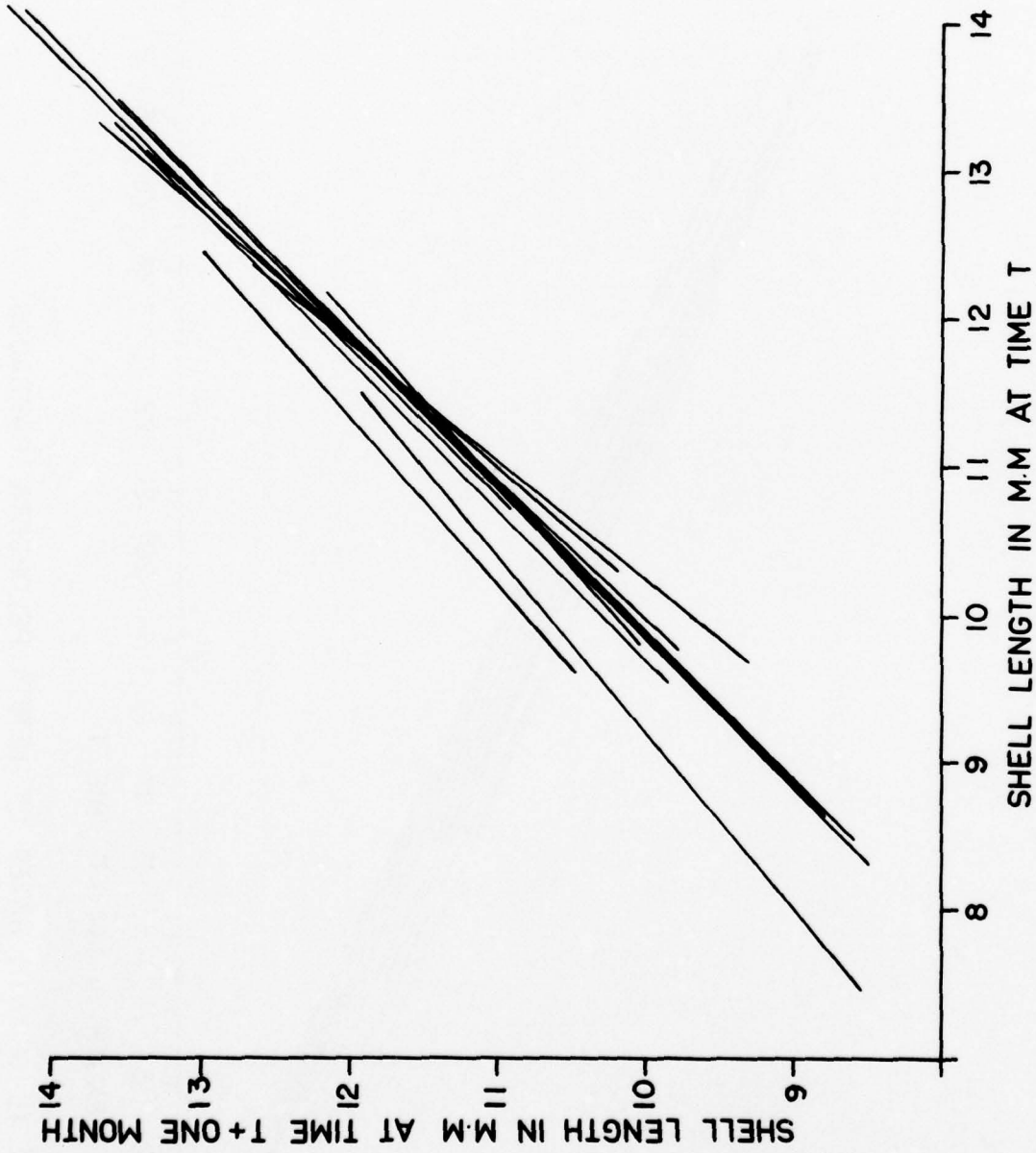
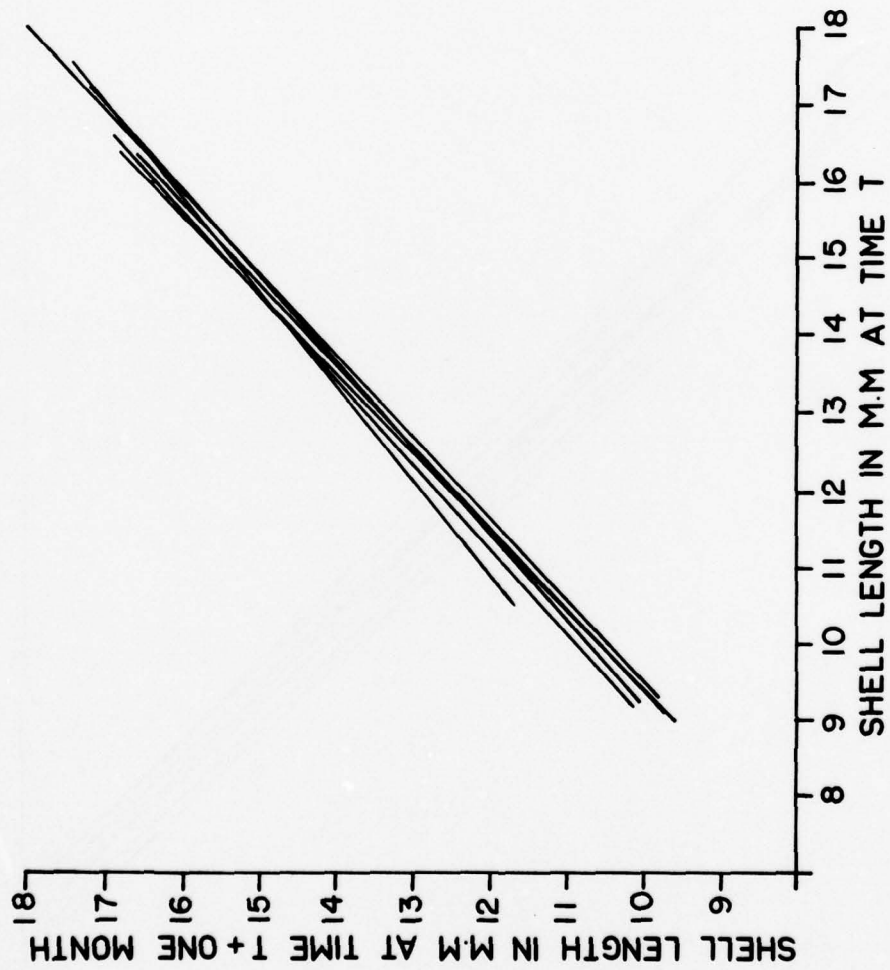


FIGURE 43 GROWTH OF *NERITA TESSELLATA*, BARBADOS.

FIGURE 4.4 GROWTH OF *NERITA VERSICOLOR*, BARBADOS.

FIGURE 45 GROWTH RATES OF *NERITA PELORONTA*, BARBADOS.

FIGURE 46 GROWTH OF *NERITA TESSELLATA*, JAMAICA.

FIGURE 47 GROWTH OF *NERITA VERSICOLOR*, JAMAICA.

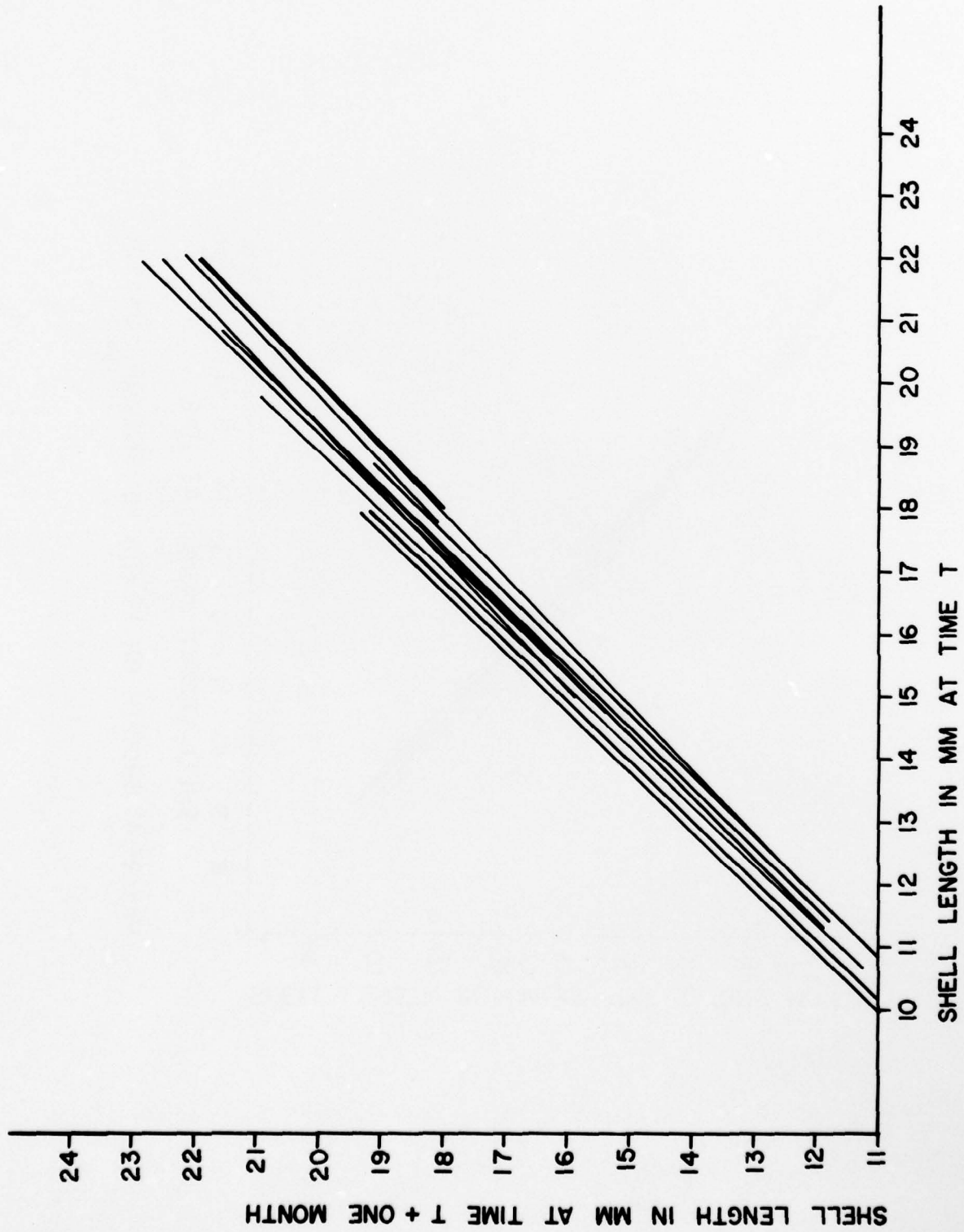


FIGURE 48 GROWTH RATES OF NERITA PELORONTA, JAMAICA.

higher than growth during the rest of the year.

The evidence for seasonal variation in growth of Nerita from Barbados, Miami and Jamaica in this study, as well as from other authors, indicates that there is a seasonal difference in Miami which is related to seasonal temperature changes; that in Jamaica there is some seasonal difference in N. peloronta; and that at Barbados there is no seasonal variation in growth rates of any of the species. In both Jamaica and Barbados the stability of growth rates may be related to the relatively small differences in mean monthly air and sea temperatures, and other environmental factors.

D. COMPARATIVE ASPECTS OF GROWTH

The interspecific differences in growth rates between the three species of Nerita in Barbados have already been noted by Axelsen (1968) and Chislett (1969). Both authors reported that N. peloronta grew fastest while N. tessellata was the slowest growing species. These differences are confirmed by the data of the present study as is presented in Figs. 39, 41 and 42. The same relationships in growth rates between the three species of Nerita in Jamaica are also illustrated in the above figures. The interspecific differences observed in Barbados and Jamaica agree with the results of Kolipinski (1964) from Miami.

A number of similarities and differences in growth rates, in patterns of growth and in population structure between Barbados and Jamaica have been noted in previous sections. Size frequency distribution histograms of Littorina are unimodal in both areas and

calculations of growth from both frequency distributions and regressions of yearly increments indicate that growth rates are similar. The presence of only a single year class in the population sample suggests that breeding is continuous or recruitment from elsewhere is continuous, and that the species is relatively slow growing. Information on growth of this species from Miami is not available for comparison.

Frequency distributions of Tectarius are unimodal in Barbados and growth is very slow in all sizes. In Jamaica, on the other hand, frequency distributions are bimodal and growth, especially in the young stages, is rapid. The Jamaican population, therefore, appears to have a definite breeding season with annual recruitment and matures quickly, while the Barbados' population is apparently composed of old slow growing animals with very little recruitment of young stages.

The size frequency distributions of Nodolittorina were clearly bimodal in Barbados, while in Jamaica the year classes were less distinct. The population thus appears to have a distinct breeding season or annual recruitment in Barbados, whereas in Jamaica the details of the population structure are less precise. The rates of growth were slow for Nodolittorina in both areas.

In the three species of Nerita the pattern of frequency distributions is highly variable. Populations of N. tessellata are bimodal in two localities in Barbados, whereas in Jamaica there is only a single year class apparent in the population sample. In Miami Kolipinski (1964) also found that the population

had a single modal value. Growth rates were relatively rapid in this species, especially in the young stages, and were slower in Jamaica than in Barbados.

Growth rates of the other two species of Nerita were also slower in Jamaica than in Barbados, while the population sample of N. versicolor showed two modes or year classes in both areas. A comparison of the monthly growth rates of the three species of Nerita in Barbados with the results of Kolipinski (1964) in Miami is shown as follows:-

<u>Species</u>	<u>Florida</u>		<u>Barbados</u>
	<u>1961</u>	<u>1962</u>	<u>March 1966-March 1967</u>
<u>N. peloronta</u> (24 mm)	.51	.58	.46
<u>N. versicolor</u> (18 mm)	.25	.54	.26
<u>N. tessellata</u> (16 mm)	.31	.19	.12

These results indicate that growth rates for the larger N. peloronta and N. versicolor were similar in both areas, but that N. tessellata grew somewhat faster in Miami than in Barbados.

Growth rates and population structure also may vary within two sites in Barbados. Differences in the presence of year classes in populations of Nerita tessellata at Little Bay and Heywood's Point have been reported by Axelsen (1968). Chislett (1969) has shown that growth rates may differ significantly between two sites in Barbados at Little Bay and Harrison's Lighthouse. Comparative regression lines for the yearly growth rates for N. peloronta

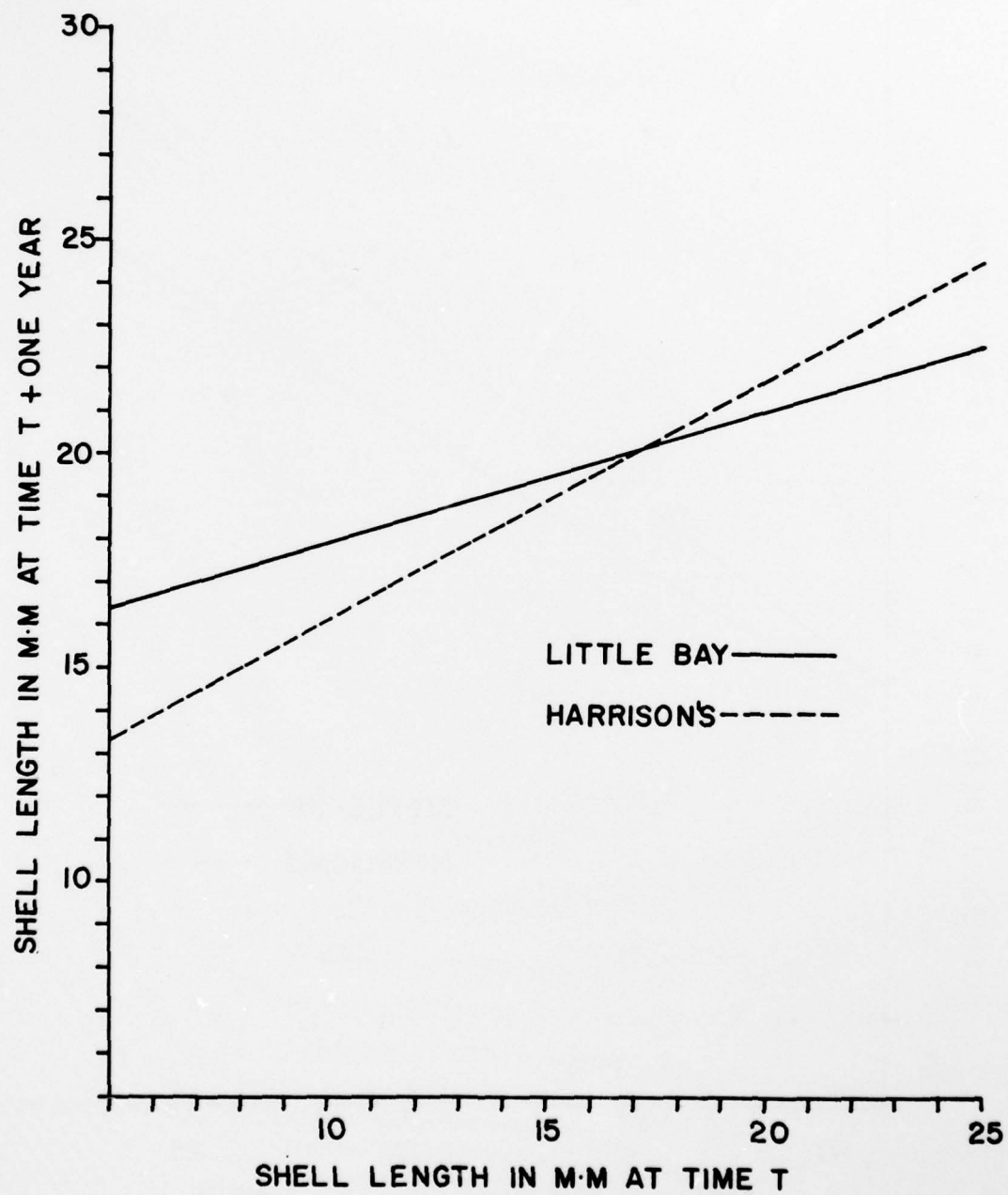
and N. versicolor are shown in Figs. 49 and 50. The regression lines for the growth rate of N. tessellata over a six month period are shown in Fig. 51.

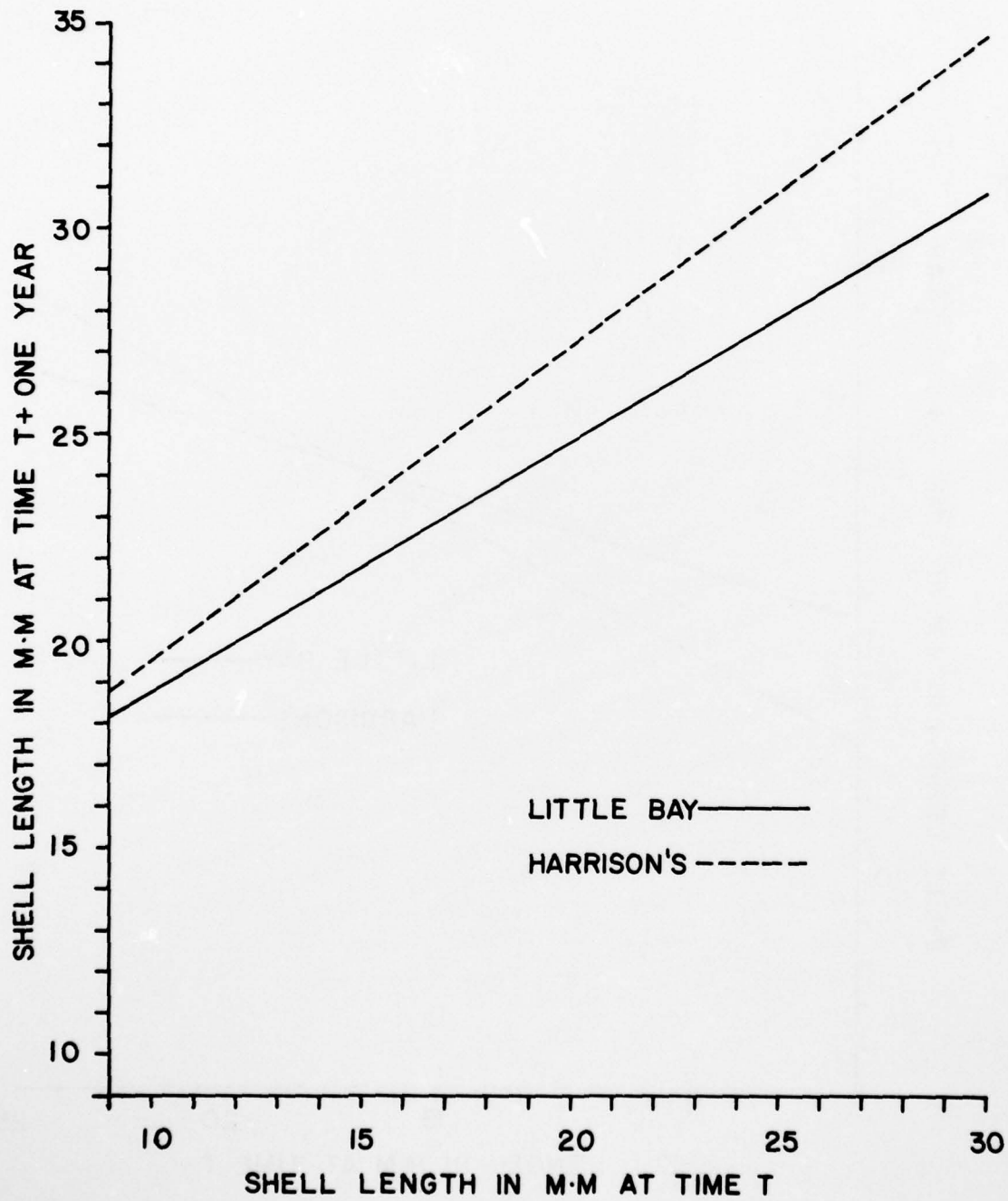
Growth rates of all species were found to be significantly greater at Harrison's Lighthouse than at Little Bay. In N. versicolor, however, animals below approximately 17.4 mm in length grew faster at Little Bay than at Harrison's Lighthouse.

The regression line for N. peloronta at Little Bay had a regression coefficient of 0.6064, and for Harrison's Lighthouse the coefficient was 0.7620. There was a significant difference between these at less than the 0.01 level. The linear regression equation for N. peloronta at Little Bay was $y = 4.42 + 0.6064x$ and the equation for Harrison's Lighthouse was $y = 8.01 + 0.7620x$.

The regression line for N. versicolor at Little Bay had a regression coefficient of 0.3074 and for Harrison's Lighthouse the coefficient was 0.5687. Again the difference was significant at less than the 0.01 level. The linear regression equation for N. versicolor at Little Bay was $y = 4.23 + 0.3074x$ and for Harrison's Lighthouse was $y = 4.76 + 0.5687x$.

In the case of N. tessellata, despite having had to use a six month growth period, the regression coefficients of the equations for Little Bay and Harrison's Lighthouse were significantly different at the 0.02 level. The linear regression equations for Little Bay and Harrison's Lighthouse were $y = 1.26 + 0.5544x$ and $y = 3.01 + 0.6093x$ respectively. It was also found that all the coefficients differed significantly from a zero value at less than the 0.01 level.

FIGURE 49 GROWTH OF *NERITA VERSICOLOR*, BARBADOS.

FIGURE 50 GROWTH OF *NERITA PELORONTA*, BARBADOS.

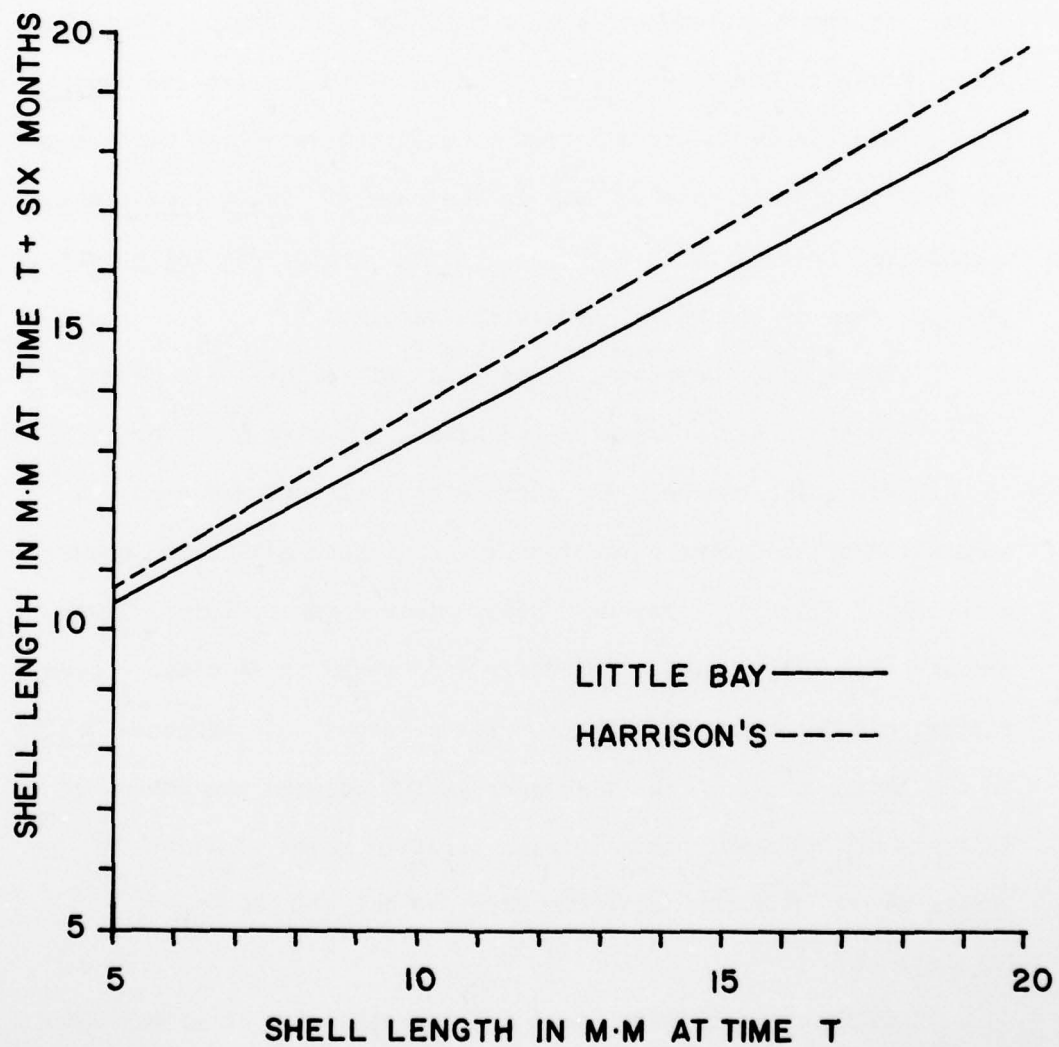


FIGURE 51 GROWTH OF *NERITA TESSELLATA*, BARBADOS.

A further comparison of growth of Nerita in Jamaica and Miami may be noted in Fig. 39 in which specimens of N. tessellata transplanted from Miami are shown to have grown faster than the native Jamaican species.

Thus in the following cases of the experimental transplanting of species from Jamaica to Barbados and Miami to Jamaica (Tectarius from Jamaica to Barbados; Nerita from Miami to Jamaica and Nerita from Jamaica to Barbados) all grew at a faster rate than did the native population samples. Only in the case of Nerita tessellata transferred from Barbados to Morant Point, Jamaica was the growth rate the same as the native population sample.

There was, therefore, a good deal of variation in growth rates between Barbados, Jamaica and Miami, and within different sites in Barbados which has been the most intensively studied area. A comparison of the climate records from Barbados and Jamaica shows a regime of slightly lower mean daily minimum temperatures, lower average rainfall, humidity and daily wind speed in Jamaica. These factors may determine the slower rates of growth of the genus Nerita in the latter area. A positive correlation between the amount of rainfall and relative humidity with relative rates of growth of Nerita at two different sites in Barbados has been shown by Chislett (1969).

Differences between Miami and the other two areas may also be related to seasonal variation in climate. However, the significant differences in growth and population structure between different sites in Barbados point to the importance of microclimatic effects

and suggest that in the areas considered microclimatic differences are equally as important as latitudinal seasonal climatic differences.

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